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THE YORKSHIRE JURASSIC FLORA

I. THALLOPHYTA—PTERIDOPHYTA

BRITISH MUSEUM (NATURAL HISTORY)

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THE YORKSHIRE JURASSIC FLORA

I THALLOPHYTA—PTERIDOPHYTA

By

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With seventy-one figures
in the text



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PREFACE

No comprehensive work on the Yorkshire Jurassic Flora has appeared since Seward's Catalogue was published in 1900, but during the years 1942-1953 Professor T. M. Harris published a series of short papers entitled *Notes on the Jurassic Flora of Yorkshire*.

It is proposed to issue a monograph in two volumes on this important flora. The present work covers the Thallophyta, Bryophyta and Pteridophyta while the second volume will deal with the Gymnospermae.

Much of the new material concerned in the monograph was collected by the author himself during the past twenty years and has been generously presented to the National Collections. Modern methods of study and technique have been used in dealing with both old and new material, and the work also includes references to records from other Museum collections.

ERROL WHITE
Keeper of Palaeontology

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INTRODUCTION

THE study of the Yorkshire Jurassic flora was begun by the founders of Palaeobotany, and many have added to it. It is the standard Middle Jurassic flora and my aim in writing this monograph has been to make the knowledge of it more available and complete. Seward did this in his catalogue in 1900, but since then more has been learnt about every species and the information has been published in upwards of a hundred scattered papers.

Advance has, however, been uneven and half the species were neglected entirely. Thus half the material in the present monograph is a compilation of published work and half is new.

HISTORY

Seward (1900) wrote a full and kindly survey of the investigation which began in 1822. At this interval it is possible to see broader features, and these I think are the inspiration of two men, Brongniart and Nathorst. Seward's catalogue was the culmination of the first and the solid foundation of the second.

Before Brongniart we have only the charming work of Young & Bird (1822, 1828). They published honest, if crude, drawings and descriptions of several plants, believing them all to be living kinds, though not all British. Their work aroused interest but was wholly surpassed by later work.

Brongniart taught us that the older fossil plants are strange and all that is known about them is what is conveyed in the description and figures. Yorkshire collectors sent him many specimens (letters are preserved in the Yorkshire Museum) and his influence is clearly seen in the figures published by Lindley & Hutton.

At this early time, John Phillips (1829) continuing the biological studies of his uncle William Smith made the geological occurrence of the plants fundamentally clear and subsequent changes have been of only secondary importance.

After about 1840 the first impulse of work on the Jurassic flora of Yorkshire slackened and each new decade up to 1900 saw only three or four papers describing new plants. Professional collectors continued, however, and many fine slabs collected by William Bean and others found their way into 'Gentlemen's Cabinets', and some of them ultimately to Museums. This fashion passed, professional collecting dwindled and died and the very localities were lost to memory. Museums were enriched but there began the unfortunate tradition that the right place for a palaeobotanist to seek material is a Museum and that precise localities (seldom fully disclosed by the professionals) were of little interest. We have still not matched many of these early specimens.

Seward's catalogue (1900) is in almost all respects the natural development of Brongniart's works; there is no fundamentally different idea or technique. To him as to others at that time

the Yorkshire compressions were 'impressions with carbon'; he knew cuticles were present, for he prepared the cuticle of *Solenites* as Murray had done seventy years before, but he did not know that such a preparation could be valuable. He also followed the normal tradition in limiting his work to the description of specimens amassed by geologists. As far as I can tell, he collected only one specimen (from Whitby).

Nathorst visited England to study this flora, in the field and in Museums, well before this (1880), but it was only after 1900 that his work and influence became important. It was then that he prepared and described cuticles (for example from *Williamsonia* flowers) which he and his colleague, Halle, had collected; the preparation of such cuticles was not new, the new idea was that their microscopic study was of interest and use. Once the microscope could be used fully, 'impressions' ceased to be automatically inferior to 'petrifications', and two vitally important results followed. The reproductive organ (often inconspicuous) became of supreme importance and the large slabs of foliage, sought for in particular by the professional collector became inadequate. Nathorst fully realised that the fossil botanist must collect and indeed alternate between field and laboratory. His own contributions to the Yorkshire flora were not numerous, but led to those of his successors in Stockholm, Halle and Florin (both of whom developed his ideas) and above all to those of Hamshaw Thomas of Cambridge who worked for some time with Nathorst and devoted much of his life to the study of this flora. Although I never met Nathorst, I regard my own work as the application of his ideas.

GEOLOGY

Geological progress in N.E. Yorkshire outstripped botanical work. As early as 1829 Phillips had recognised an 'Upper' and 'Lower' Estuarine Series separated by marine incursions, and soon after he recognised a second incursion, the Millepore Bed, when he distinguished a 'Middle' Estuarine Series. Later still a third marine incursion was recognised, the Ellerbeck Bed, but this led to no change of names of the plant-bearing rocks. In 1892 the Geological Survey of the area was completed (Fox-Strangways) and no considerable alteration has since been made. The memoir of Wilson (1948) differs chiefly in omitting much local detail. Arkell (1933) summarises progress.

The plant-bearing rocks have already been described in outline (Harris, 1952, 1953) and only the briefest summary will be given here. A full account will be given in the second part of this monograph when the description of the plants is complete.

Almost all the plants are found in the freshwater rocks which have long been called the 'Estuarine Series', but as they are purely deltaic the term 'Deltaic Series' has been substituted and is used here. The following table is based on Hemingway (1949):

- Marine Oxfordian, many zones.
- Marine Callovian, *macrocephalus* zone.
- Freshwater Upper Deltaic (= Upper Estuarine).
- Marine 'Grey' or 'Scarborough' Limestone, *blagdeni* zone.
- Freshwater Middle Deltaic Gristhorpe Series (= Middle Estuarine).
- Yons Nab Marine Series.
- Marine Millepore Bed and Whitwell Oolite, possibly *discites* zone.
- Freshwater Middle Deltaic Sycarham Series (= part of Lower Estuarine).

Marine Eller Beck Bed and Hydraulic Limestone (not zoned).
Freshwater Lower Deltaic (= Lower Estuarine).
Marine 'Dogger', various zones locally including *murchisonae*, base of Oolite.
Marine Blea Wyke Beds, Yeovilleian, Upper Lias.
Marine Lias, Whitbian and many other zones.

It will be seen that none of the four Deltaic Series can yet be related precisely to marine zones, but the three lower must belong to the Bajocian and the Upper Deltaic to the Bathonian. It must be pointed out also that the marine intercalations (apart from the Scarborough Limestone) are all local, and so the freshwater rocks are by no means everywhere divided. A final point is that the word 'dogger', properly an ironstone concretion, is used in Britain for the variable marine rocks of coastal origin between Lias and Lower Deltaic; but elsewhere it is extended to cover the whole of the Lower Oolites.

THE FUTURE

The present work aims to be complete in the same way as that of Seward (1900); it deals with all the available specimens by the available technique. Knowledge of every species in the flora still shows obvious gaps caused partly by the lack of the necessary specimens, and partly no doubt by the failure to get the fullest information from existing material. Vigorous collecting should begin again generally, and more powerful methods might also be used. There must be many rich beds in the upper parts of the great cliff section south of Whitby; they might be tackled with explosives by a man suspended by ropes—but this, alas, I must leave to someone younger.

I am sure that spectacular advance will be made by collectors with fresh ideas, and I am convinced that it is the collector rather than the locality which is exhausted.

Fifty years of progress by the application of Nathorst's ideas have made the old catalogue out of date. May I express the hope that progress in the next fifty years will be quicker?

TOM M. HARRIS

SYSTEMATIC DESCRIPTIONS

Thallophyta

Algae

Fossils under the name *Fucooides* have been reported from the Deltaic Series, but all of them must now be regarded as liverworts. True algae are few and ill-known but not merely through neglect, for many small specimens have been examined as possible algae which proved either to be fragments of larger plants or too characterless to merit any description. The specimen mentioned below is the only one regarded as convincingly of algal nature and even it is of little scientific interest.

Artificial group name ALGACITES Schlotheim, 1822 : 43

Algacites sp.

Text-fig. 1 A-C

DESCRIPTION. Thallus cylindrical, composed of filaments about 15–20 μ wide; filaments organised into a longitudinally running set forming a medulla surrounded by an originally cylindrical cortex of short horizontal branches. Medulla about 1 mm. wide, cortex 0.5 mm. wide; filaments freely branched by almost equal forking; not constricted; not showing any specialised cells; septa not visible; apices of cortical filaments acute, not showing any hairlike prolongation.

MATERIAL. One specimen only (V.30916) from Cloughton *Otozamites beani* Bed; Middle Deltaic (Sycarham Series).

REMARKS. The specimen was made into a balsam transfer, and only studied in that state. The filaments are seen very clearly but it is not possible to make out the thickness of the wall nor any septa that may have been present. A filament is figured which shows what may be rather short cells. There is no sign of mucilage around the filaments, nor of any specialised reproductive or other bodies. The upper end of the specimen looks as though it were forked but the evidence for this is not conclusive.

The specimen seems to be more comparable with *Chaetophora incrassata* of the freshwater Chlorophyceae than any other Recent alga but this assumes that its filaments were septate; another difference is that the filaments of the fossil are a good deal thicker. Comparison is also possible with such marine algae as young plants of *Codium*, or of the Rhodophycean *Nemalion*.

Fungi

Text-fig. 1 D, E

Many Yorkshire leaves show signs of local injury in the form of a rupture in one epidermis and a considerable increase in the thickness of internal coaly matter around this rupture. It is not possible to demonstrate any spores by direct observation or by maceration, nor any cellular tissue in the coaly pad. Some of these injuries certainly occurred while the leaves were alive, as there are signs of reaction such as local cell division or cutinisation of the inner walls of surrounding cells.

There is no reason to suppose that all these injuries are of the same nature and without additional information they may be of little interest. It is likely that many are caused by leaf fungi forming spores, and sometimes little sclerotia, just under the epidermis; some are probably parasites and others (where no cell reaction is visible) probably saprophytes.

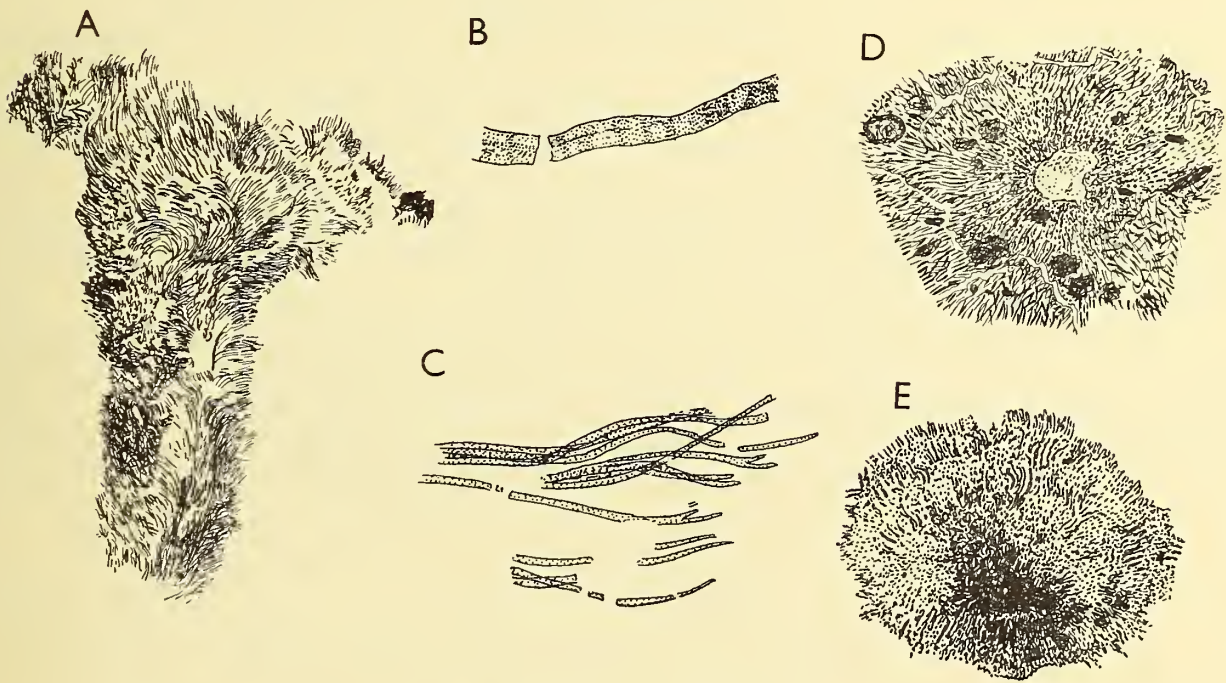


Fig. 1. *Algacites* sp., Leaf spot fungus

A, *Algacites* sp. as seen in transfer (drawing on photograph). Not all the filaments are shown, V.30916, $\times 20$. B, filament of same showing possible septa, $\times 200$. C, cortical filament from same specimen, $\times 100$. D, leaf spot fungus on *Phlebopteris polypodioides*, V.32505, $\times 200$. E, similar leaf spot fungus, V.31952, $\times 200$.

A-C, from Cloughton *Nilsson* Bed; D, E, Gristhorpe Bed.

Such local injuries are to be seen on most kinds of leathery leaves, e.g. *Ctenis*, *Ctenozamites*, *Nilssoniopteris*, *Eretmophyllum* and *Bilsdalea*, and their frequency at Gristhorpe is about one such injury per two or three square centimetres of isolated leaf studied. These injuries might also be caused by sucking insects.

More satisfactory evidence of leaf fungi is provided by the specimen shown in Text-fig. 1D.

It is one of a large number of similar spots on the lamina of a pinna of *Phlebopteris polypodioides* from Gristhorpe. The specimen is one which had undergone natural maceration before preservation and scarcely anything remains but the two epidermises and the veins, and here the delicate brown film of the fossil shows very conspicuous spots. On transferring the lamina it was possible to see that the spots consist of radiating hyphae about $1-2\mu$ thick. They are situated between the two epidermal membranes and in a few specimens (though not in the one figured) there is a small break in the upper epidermis in the middle of the fructification. No spores were seen.

While this fungus is strictly unclassifiable without closer knowledge, it is closely similar to many genera of the Sphaeropsidales, the common leaf spot fungi. Such fungi are familiar in the Tertiary but have not been much observed in the Jurassic.

Bryophyta

No moss-like fossil has ever been found in the Yorkshire Deltaic Series. Hepaticae occur, but they are rare and form inconspicuous fossils in which the substance is reduced to a very delicate film which itself often forms the plane of cleavage instead of the cleavage passing over its surface. It must be admitted that the Hepaticae so far discovered in the Deltaic Series are unsatisfying fossils since they fail to contribute the information which is so much needed to elucidate the inter-relationships of the existing families.

Thalloid fossils have been classified under many generic names recalling particular marine algae or terrestrial hepatics. Few of these names are defensible and Walton's proposal (1925: 565) to name all those which showed characters exclusive to the hepatics as *Hepaticites* and those which agreed equally with algae as *Thallites* meets present needs. Certain other genera have been proposed by Lundblad (1954) for rather better material.

HEPATICAЕ

Genus HEPATICITES Walton, 1925 : 565

The following thalloid plants resembling liverworts are known in the Yorkshire flora:

(1) Thallus branches narrow (3-4 mm.)	<i>Hepaticites arcuatus</i>
Thallus branches wider	2
(2) Air chambers probably present	3
Air chambers absent	4
(3) Ventral scales obvious	<i>Hepaticites haiburnensis</i>
Ventral scales not obvious	<i>Hepaticites wonnacotti</i>
(4) Lamina very delicate, one-layered	<i>Hepaticites hymenoptera</i>
Lamina more robust	<i>Thallites</i> sp.

The fact that most of these species are rare and represented by a single specimen suggests that more may await discovery, and it is possible that *Furoides arcuatus* Phillips (5 mm. wide), and *F. diffusus* Phillips (3 mm. wide), both ill-known, may be further species.

Hepaticites arcuatus (L. & H.) Harris

Text-fig. 2 A-F

- 1836 *Fucoides arcuatus* Lindley & Hutton, p. 93, pl. 185. (Poor figure.)
 1864 *Fucoides erectus* Leckenby, p. 81, pl. 11, fig. 2a, b. (Good thallus. Referred to in text as figs. 3a and 3b. Fig. 2a is Leckenby Collection, K1, Sedgwick Museum, Cambridge.)
 1869 *Haliseris erecta* (Leckenby) Schimper, p. 185.
 1875 *Fucoides erectus* Leckenby: Phillips, p. 196, lign. 3. (From Leckenby (1864). Not *F. arcuatus*, p. 3, lign. 1.)
 1898 *Marchantites erectus* (Leckenby) Seward, p. 233, text-fig. 49. (As Leckenby, 1864.)
 1900 *Marchantites erectus* (Leckenby): Seward, p. 49, text-fig. 2 (as Seward, 1898, text-fig. 49), pl. 19, fig. 2. (Form of thallus.)
 1925 *Thallites erectus* (Leckenby) Walton, p. 564. (Name.)
 1942 *Hepaticites arcuatus* (L. & H.) Harris, p. 394, text-fig. 1. (Cellular details.)
 1954 Cf. *Marchantites erectus* (Leckenby): Medwell, p. 80. (Australia.) No figures.

Seward (1900) cites a few other references but without figures.

EMENDED DIAGNOSIS. Plant thalloid; thallus flat except at extreme margin which may curve downwards; margins entire. Branching by equal dichotomy at intervals of 5 mm.—1 cm.; branches divergent. Width of thallus 3–4 mm.; thallus composed of a midrib up to one millimetre wide and a delicate lamina, midrib thicker and well marked, but not abruptly divided from lamina. Lamina not divided into chambers or areas, composed of about three sets of cells of which one conspicuous set is about 40μ wide, another conspicuous set is about 80μ wide, and other cells ill-marked; the more conspicuous cells forming arching rows running forwards near the midrib and bending outwards. Extreme edge of lamina one cell thick only. Midrib probably composed of several additional cell layers; cells elongated. Ventral scales absent. Rhizoids rather few, slender and unbranched, straight, arising from the midrib, thin walled. Reproductive organs unknown.

HOLOTYPE. Specimen figured Lindley & Hutton (1836, pl. 185).

DISTRIBUTION. Occasional in the Gristhorpe Series of the Middle Deltaic. Four localities: Gristhorpe Bed; Cloughton Wyke *Solenites* Bed (recorded by Leckenby and by Phillips); Cloughton Wyke *quinqueloba* Bed; Fryup Dale, old coal pits.

DISCUSSION. Though frequent at Gristhorpe it is seldom well preserved and the specimens are commonly no more than a faint brown stain, but they show their cellular details well in transfers or when immersed in oil. Some of the specimens are so large that they look as though they were preserved in the position of growth, creeping over a soil surface.

No reproductive organs were recognised and although several new specimens have been studied they merely confirm what was stated in 1942. The new transfers show the cells rather better and are figured here. *H. arcuatus* may be attributed on the basis of the form of the thallus, the structure of the lamina and of the rhizoids to the Jungermanniales Anacrogynae, allied to *Pellia*.

COMPARISON. *H. arcuatus* resembles several other Mesozoic liverworts and does not contribute any important information. The most similar are:

Hepaticites laevis Harris 1931 (basal Lias of Greenland) with far more numerous rhizoids.
Thallites yabei (*Marchantites yabei*) see Kryshstofovich (1930: 144; 1933: 127) and Oishi (1940: 183) a slightly larger and less branched plant from the Lower Jurassic rocks of Siberia and Japan. Its microscopic structure is unknown, but there is a suggestion of a similar arrangement of cells.

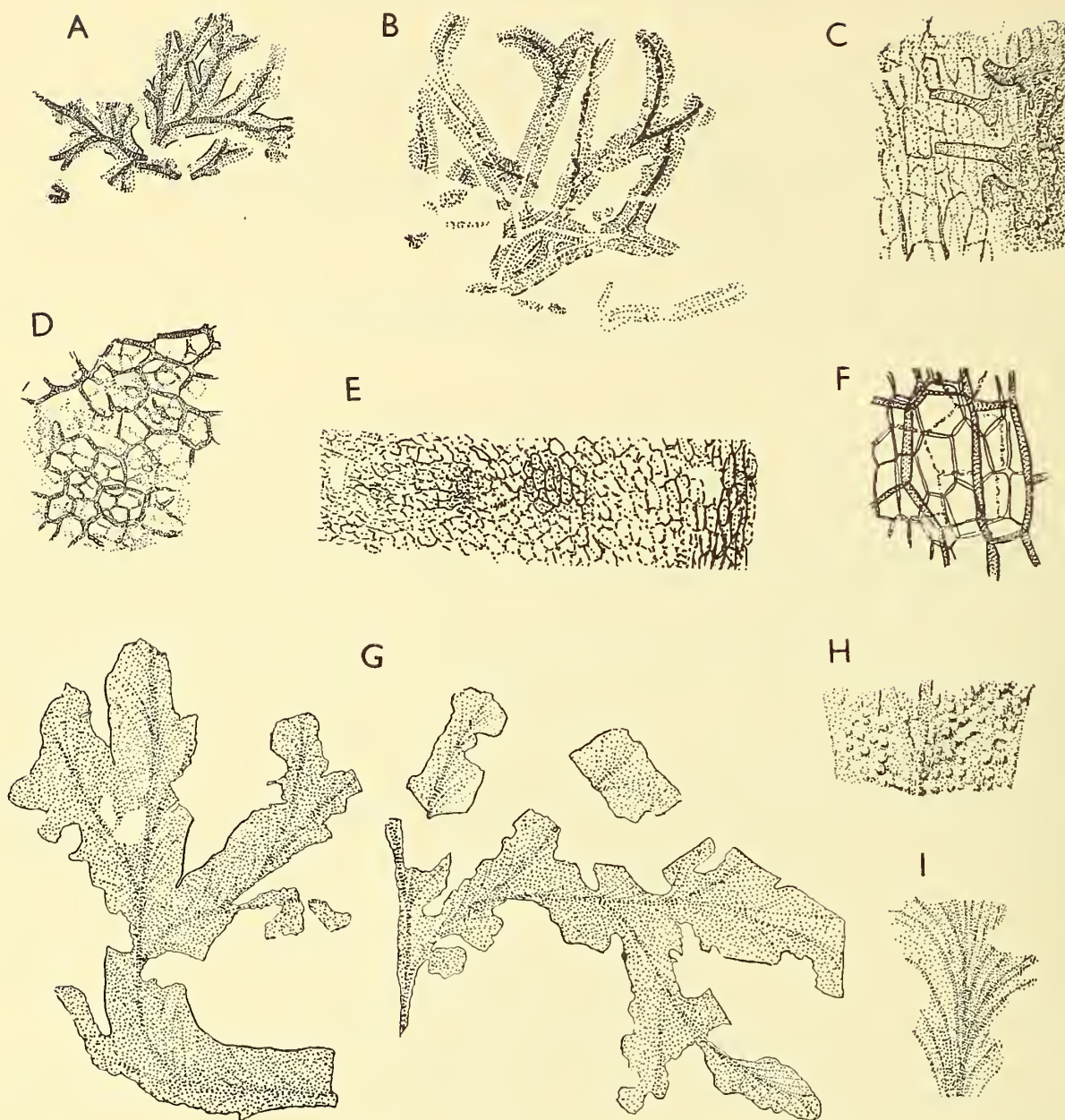


Fig. 2. *Hepaticites arcuatus* (L. & H.), *H. wonnacotti* Harris

A-F, *Hepaticites arcuatus*. A, rather closely branched thallus, V.25848, $\times 1$. B, rather distantly branched thallus, V.31047, $\times 1$. C, transfer of edge of midrib showing rhizoids, V.24683, $\times 100$. D, transfer of lamina showing superimposed cells, V.24683, $\times 100$. E, transfer extending from the midrib (right) to the margin (left) showing the prevailing orientation of cells, V.30918, $\times 80$. F, semi-diagrammatic drawing of lamina in transfer showing three sets of cells, V.24683, $\times 200$.

G-I, *Hepaticites wonnacotti*. All from the holotype, V.26833. G, thallus fragments, $\times 1$. H, older part of thallus coated with NH_4Cl to show the surface bulges, $\times 2$. I, thallus apex (in oil) to show the ribs, $\times 2$. All the specimens are from the Gristhorpe Bed. B and E are new figures; the others are from Harris (1942).

Thallites zeilleri (Seward, 1894: 18) from the English Wealden; a plant looking just like *H. arcuatus* but of unknown microscopic structure.

Thallites uralensis Kryshtofovich & Prinada (1933: 7); a very similar looking Lower Jurassic plant of unknown structure.

Lundblad (1954) mentions some other species of *Thallites*.

Two specimens described by Phillips (1875) possibly belong to *Hepaticites arcuatus* but are here regarded as distinct but indeterminable. They are:

'*Fucoides arcuatus*' (p. 195, lign. 1); a distinctly broader thallus, apparently with no midrib.

I have never seen a specimen of the present species which approaches that figure in either respect.

'*Fucoides diffusus*' (p. 196, lign. 2); the thallus is of similar width to *H. arcuatus* and branches similarly but the lamina is lobed. The original specimen (in the Yorkshire Museum) suggests that it really undulates upwards and downwards and so is a good deal broken by the bedding plane but may not be truly lobed. I have not seen any specimen of *H. arcuatus* which shows an approach to this undulation.

Hepaticites wonnacotti Harris

Text-fig. 2 G-I

1942 *Hepaticites wonnacotti* Harris, p. 397, text-fig. 2.

DIAGNOSIS. Plant thalloid; thallus about 12 mm. broad; dichotomizing at intervals of 1.5–2 cm. Thallus flat, apart from numerous low bulging areas about 1 mm. wide in the lamina. Lamina composed of several layers of cells which are polygonal and thin-walled over most of the lamina but elongated and thicker walled along the midrib. Midrib present but ill-defined, rib-like strands arising from the midrib and traversing the lamina. Long unicellular rhizoids, 40 μ wide, produced in considerable numbers along the midrib.

HOLOTYPE. V.26833.

DISTRIBUTION. Only known from the Gristhorpe Bed, Middle Deltaic.

DISCUSSION. The evidence provided by the rather large size of the thallus; its surface bulges (which may represent air chambers) and the arching ribs all suggest classification in the Marchantiales. Failure to find tuberculate rhizoids, however, and the fact that no ventral scales were seen is evidence against this. It may be tentatively classified in the Marchantiales.

COMPARISON. *Hepaticites wonnacotti* is larger than most Mesozoic liverworts. It resembles *Thallites rostaffinskii* Raciborski (1894: 10) from the Keuper of Poland but though this has been supposed to show Marchantiaceous air chambers they are far smaller than those of *H. wonnacotti* and are most likely the epidermal cells of an unchambered thallus (see Lundblad, 1954).

Thallites marchantiaeformis (Sap.) from the uppermost Jurassic of Portugal is of similar size but entirely unknown structure (see Teixeira, 1948:25).

Hepaticites haiburnensis sp. nov.

Text-fig. 3 B-D

DIAGNOSIS. Plant thalloid; thallus flat, margins entire. Branching by equal dichotomy at intervals of about 1 cm.; branches divergent. Width of thallus about 8 mm., thallus composed of an ill-defined thickened midrib gradually passing into a lamina which becomes increasingly

delicate towards the margins. Lamina many cells thick, epidermal cells about $70\mu \times 50\mu$; showing obscure outlines suggesting obliquely placed air chambers 500μ long, 200μ wide; (pore not recognised). Midrib bearing two rows of conspicuous ventral scales, ventral scales, 2.5 mm. wide, occurring at intervals of about 1 mm. Rhizoids numerous, arising on midrib, about 40μ wide (details of wall not known). Reproductive organs unknown.

HOLOTYPE. V.30917.

DISTRIBUTION. *H. haiburnensis* is represented by the holotype alone. It occurred in a fallen block at the foot of the Haiburn plant bed, almost certainly fallen from its upper part. Its associates are *Clathropteris obovata* and *Neocalamites hoerensis*, and it belongs to the Lower Deltaic Series.

DISCUSSION. The specimen in the dry state shows the ventral scales alone, the lamina is only visible when mounted in oil. It shows a number of distinct branches which may well have been originally joined but nothing remains to unite them: this recalls Walton's (1949) discovery of isolated branches of liverwort-like plants radiating from a point and suggests that the plant is preserved in the position of growth. The evidence for *H. haiburnensis* as it is a single specimen is, however, less conclusive.

The fact that the ventral scales, though originally no doubt one cell thick, are more conspicuous than the rest of the thallus is not altogether surprising, for such scales are often loaded with dark coloured tannin-like matter. I have found by experiment with *Plagiochasma* (which has scales of similar shape) that when a thallus rots under water the scales are among the most resistant parts.

All that is known of the air chambers of the thallus is a series of polygons faintly visible when the fossil is moistened in oil; they were no better seen in transfer preparations. Some show a dark spot which might represent an air pore but this is not convincing.

H. haiburnensis can be confidently classified in the Marchantiales and probably the Marchantiaceae. It shows two characters found in the Marchantiales alone; a particular type of ventral scale and probable air chambers. Unfortunately it cannot be classified much further because these organs occur at least in a modified form throughout the family. In the Recent Ricciaceae the mature ventral scales though varied in appearance never look much like those of *H. haiburnensis*, nor does one see large and apparently simple air chambers in the thallus. These characters are, however, widespread in the Marchantiaceae.

More than half the genera have almost exactly similar ventral scales, and several have large, simple air chambers much as *H. haiburnensis* seems to possess. The two features together occur for example in *Targionia* and in *Preissia*, genera which are classified at opposite ends of the Marchantiaceae. Further classification is indeed impossible without better material giving knowledge of its reproductive organisation.

Lundblad has described some better characterised Marchantiaceous liverworts, *Marchanteolites* (1954) for a thallus with air pores, and *Marchantites* (1955) for a thallus with the air pores and other characters of the group Marchantiaceae. The present specimen (with no information about air pores) fits neither genus, and is therefore left in the non-committal *Hepaticites* till more is learnt.

COMPARISON. The only fossil liverworts with ventral scales are much younger, *Marchantites sezannensis* from the Tertiary of Paris and *M. hallei* from the Cretaceous of Patagonia. Both have air pores and other characters not available in *H. haiburnensis*.

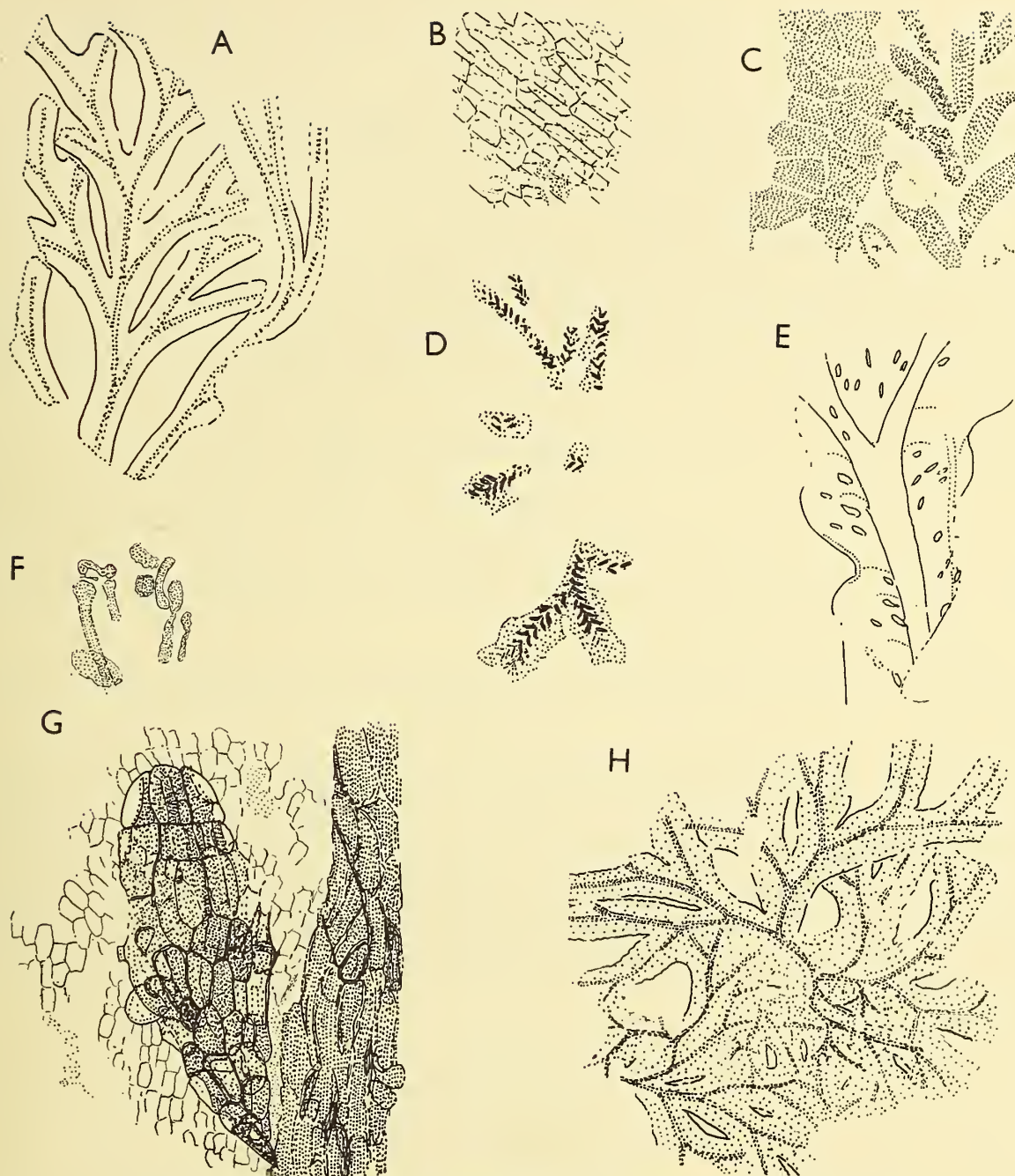


Fig. 3. *Thallites* sp., *Hepaticites haiburnensis* sp. nov., *H. hymenoptera* sp. nov.

A, *Thallites* sp. The branches on the right are crushed obliquely and badly seen. K479, Sedgwick Museum, Cambridge, $\times 1$. Scarborough.

B, *H. haiburnensis*, marginal part of the thallus, holotype, V.30917, $\times 50$. Haiburn Wyke. C, part of the same thallus showing ventral scales on the right and indistinct cracks in the lamina which are possibly air chambers, $\times 8$. D, drawing of the holotype showing ventral scales on a number of distinct branches, $\times 1$.

E-H, *H. hymenoptera*. E, transfer of lamina showing undulating margins, dark plates and folds (dotted lines), V.32502, $\times 4$. F, rhizoids, V.32503, $\times 100$. G, thallus in transfer showing midrib tissue on right, cells of lamina to left and one of the dark plates, V.32502, $\times 100$. H, some of the thallus exposed on the holotype (specimen observed under oil), V.32501, $\times 1$. All from Gristhorpe Bed.

Hepaticites hymenoptera sp. nov.

Text-fig. 3 E-H

DIAGNOSIS. Plant thalloid; thallus flat, margins entire or undulating irregularly. Branching by equal dichotomy at intervals of 1.0–1.5 cm., branches divergent. Width of thallus 6–7 mm., thallus composed of a midrib 1 mm. wide and a very delicate lamina; midrib thickened and sharply distinguished from the lamina. Lamina uniform in the main but shows oblique folds and dark plates. Lamina composed of a single layer of uniform cells, about 40–60 μ by 20 μ broad, long axis inclined to midrib at an angle of 10°–30° near midrib but at about 45° near margin. Cells shorter near margin and almost isodiametric. Cell walls thin, straight, uninterrupted by pits; cell corners not thickened, cell surface unspecialised. Occasional lines of cells of lamina forming a fold or ridge inclined at 30°–45° to the midrib (nature of fold unknown). Occasional dark plates (? gemmae) situated on lamina, mostly near midrib. Plates typically 500 μ long \times 200 μ broad, long axis inclined to midrib at 30°–45°. Plates showing thick-walled cells up to 100 μ \times 50 μ ; and additional smaller cells in the middle region. Margins of plates free from lamina, at least in part. Midrib moderately thick, composed of several layers of obscurely marked elongated cells. No ventral scales apparent. Rhizoids arising from enlarged cells of midrib, simple, unbranched; width about 15 μ ; walls rather delicate and apparently not tuberculate.

HOLOTYPE. V.32501 (Text-fig. 3 H).

DISTRIBUTION. Only known from the Gristhorpe Bed, Gristhorpe Series of Middle Deltaic. Rare.

DISCUSSION. A few fragments agreeing with *H. hymenoptera* have been previously met at Gristhorpe, but nothing worth description. In 1954 three large plants were found close together and on the same bedding plane, looking much as though in the position of growth. They are so delicate as to be almost invisible till the rock is moistened. The holotype (Text-fig. 3 H) shows part of one of these plants, some of the branches are overlapping and confused, but others separate and clear. A second specimen was unfortunately destroyed in preparation, a third was used successfully for celloidin transfers and is shown in Text-fig. 3 E–G. In the holotype most of the substance has adhered to one side (the part), but some to the counterpart, making study more difficult. The transfers show convincingly, however, that the lamina is but one cell thick, the cell outlines being sometimes very clear indeed. All specimens show dark spots ('plates') on the lamina. In transfer these appear to be on one surface only (probably the upper) and consist of more than one cell layer. Some of the cells are larger than those of the lamina. These 'plates' were compared with the star-shaped gemmae of *Blasia pusilla* (where they occur scattered on the underside near the midrib). They seem less like the erect leafy plates of *Petalophyllum* and the ventral scales of Marchantiales, in both of which they are much more regular in size and position. It is unknown how they were attached. The rhizoids were only seen in the transfer of the midrib of the counterpart, which presumably therefore represents the lower side; no plates were seen on this side. (Unfortunately, it was not noted in the field whether part or counterpart was above.)

Such a species as *H. hymenoptera* is only classifiable on the convenient but baseless assumption that the Jurassic Hepaticae were very much as those of today: on this assumption *H. hymenoptera* would be a member of the Jungermanniales anacrogyneae rather close to *Blasia*.

COMPARISON. *Hepaticites hymenoptera* is distinctly larger than *H. arcuatus*, the much more delicate lamina sometimes shows its single layer of cells even before being transferred. *H. arcuatus* has no dark 'plates'. *H. wonnacotti*, a larger plant, has a lamina more than one cell thick, as has *H. haiburnensis*. '*Thallites* sp.' is similar in size to *H. hymenoptera* and its structure is unknown, but it must have been much more robust; a thallus as delicate as that of *H. hymenoptera*, which is hard to see even on the ideally fine Gristhorpe Bed matrix, would be invisible in a sandstone.

The only species in other floras definitely proved to have a one-layered lamina are *H. glebosus* Harris (1931) from the Lower Lias of Greenland, a more slender plant with characteristic swellings on its rachis, and two species, *H. lobatus* and *H. metzgerioides* Walton (1928), both much smaller plants, from the British Coal Measures. The name *hymenoptera* refers to the membranous wing along the midrib.

Genus THALLITES Walton

Thallites sp.

Text-fig. 3 A

The figured specimen is the only one of its kind known and consists merely of a brown iron stain in a very hard nearly pure silica sandstone and no fine details are visible. The midrib, however, forms a conspicuous and darker ridge, particularly in the lower parts.

The specimen (K.479) is in the Sedgwick Museum, Cambridge and is labelled '*Sphenopteris digitata*, Scarboro', '90 Nr. Carnelian bay'. It is a rounded beach pebble and the locality indicates an Upper Deltaic origin. A small proportion of the beach pebbles are glacial erratics but the intensely hard sandstone is a matrix which is characteristic of the Upper Deltaic and there is no reason to doubt this origin.

Thallites sp. is comparable with many specimens described under different specific names, seven of which are listed by Lundblad (1954:408) and another figured and described by Prinada (1938) as *T. polydichotomus*. Its value is merely to record the occurrence of a fairly large probable liverwort in the Upper Deltaic but its investigation must await better material.

Pteridophyta

EQUISETALES

The nine known species of the Yorkshire Jurassic Equisetales are distinguished below. (This key would not deal with every specimen.)

- | | | |
|--|----------------------------|---|
| (1) Leaves united basally into a tubular sheath; stem interior smooth | (<i>Equisetum</i>) | 2 |
| Leaves free or in groups diverging at the base, stem interior with longitudinal ridges | | 3 |
| (2) Stems usually 10 cm. wide, diaphragm a smooth disc | <i>Equisetum beani</i> | |
| Stems usually 4-6 cm. wide, diaphragm a smooth disc | <i>Equisetum columnare</i> | |
| Stems usually 2 cm. wide, diaphragm with radiating spokes | <i>Equisetum laterale</i> | |
| Stems under 1 cm. wide | <i>Equisetum</i> sp. A | |
| (3) Diaphragms of main stem with radiating spokes, leaves unknown | <i>Calamites rotifer</i> | |
| Diaphragms of main stem unknown or absent, stem with diverging leaves | | 4 |

- | | | |
|--|--------------------------------|---|
| (4) Leaves united in two or more groups | <i>Schizoneura stenophylla</i> | |
| Leaves free at base | | 5 |
| (5) Leaves about 3 cm. long, 3-6 mm. wide, margins jagged (main stem unknown) | <i>Annulariopsis simpsoni</i> | |
| Leaves at least 5 cm. long, 1-2 mm. wide, margins entire, main stem with longitudinal ridges | (<i>Neocalamites</i>) | 6 |
| (6) Stems up to 2 cm. wide; ridges only conspicuous on larger stems, about twice as numerous as leaf scars | <i>Neocalamites nathorsti</i> | |
| Stems up to 5 cm. wide; ridges conspicuous on all stems, about three times as numerous as leaf scars | <i>Neocalamites hoerensis</i> | |

Genus EQUISETUM Linnaeus

1833 *Equisetites* Sternberg, p. 43.

Different authors have used the names *Equisetum* and *Equisetites* for fossils they considered like *Equisetum*. I have previously followed Seward and used *Equisetites*; the different name seemed to be a useful convention for noticing the different way in which Recent plants and fossils are available for study. Latterly, however, several authors have deliberately used the names of living genera for Mesozoic plants (almost all do so for Tertiary ones), and as the convention is not kept it is best dropped. A separate name should, however, certainly be used whenever there are two or more Recent genera with which the fossils could be identified with equal justice, for here the name of the fossils has a wider (and thus different) connotation from that of the living genera. No morphological difference has ever been proved between *Equisetum* and *Equisetites*, indeed progress in knowledge adds new points of agreement. Most of the Mesozoic species differ in their much greater size of stem, but this is apparently not accompanied by any anatomical difference from the Recent ones.

The cuticles of three of the species described here agree well with those of Recent species of *Equisetum*. When prepared in the ordinary way, the Recent cuticle has indeed a very different aspect, because it is heavily and conspicuously ornamented with silica, but when this is removed, the cuticle (which loses its striking appearance) becomes more like that of the fossils. It is assumed that the silica has dissolved out of the fossil, leaving only obscure bulges or little pits, especially in the stomata, where a silica nodule has disappeared. These features are better seen using phase contrast microscopy than with ordinary lighting. It has not been possible, however, to match the trichome bases of *Equisetum* sp. A. in a Recent species.

The Yorkshire species are compared below.

1. *Stem*.

E. beani, typically 10-12 cm. wide with 100-150 leaves and slightly contracted nodes; vascular strands of internode somewhat woody. (Cuticle unknown.)

E. columnare, typically 4-6.5 cm. wide with 50-80 leaves and slightly expanded nodes; internodes without woody strands. Stomata large (100 μ or more long).

E. laterale, typically 1-3 cm. wide with 25-35 leaves; nodes equalling internode, internode without woody strands. Stomata smaller than in *E. columnare* (50 μ long).

Equisetum sp. A., typically 1-4 mm. wide with 5-8 leaves.

2. *Leaf sheath*.

E. beani, not known.

E. columnare, commissural furrows typically 2-3 cm. long, wider than the leaf segments at the top; free leaves 2-4 mm. long.

E. laterale, commissural furrows typically 1 cm. long, narrower than the leaf segments at the top; free leaves 7–12 mm. long.

Equisetum sp. A., leaf sheath short, free leaf not known.

3. *Nodal diaphragm*.

E. beani, robust, smooth with a ring of tubercles.

E. columnare, fragile, only small ones found isolated; smooth with a ring of tubercles.

E. laterale, robust (often rotating in compressed stem); form of a wheel with rim, spokes and hub.

Equisetum sp. A., not known.

Equisetum columnare Brongniart

Text-figs. 4, 5 E, F, I, J

1. Yorkshire specimens:

1822 'Reed or Cane', Young & Bird, p. 184, pl. 3, fig. 3. (Erect stem.)

1828 'Reed or Cane', Young & Bird, p. 193, pl. 3, figs. 4–6. (Erect stems.)

1828 *Equisetum columnare* Brongniart, p. 115, pl. 13. (Erect stem.)

1829 *Oncylogonatum carbonarium* König, p. 300, pl. 32. (Erect stems, ? both from Yorkshire, also compressed leaf sheath fragments from Brora, Scotland.)

1873 *Equisetum columnare* Brongn.: Saporta, p. 254, pl. 30, fig. 5. (Erect stem, said to be from Scotland, but there is no evidence that stems are preserved in this way in Scotland.)

1875 *Equisetites columnaris* (Brongn.) Phillips, p. 197, lign. 4; ? not lign. 5. (Rough figure of node.)

1898 *Equisetites columnaris* (Brongn.): Seward, p. 72, text-fig. 11. (Erect stems in matrix, figure inverted); p. 269, text-fig. 58. (Node.)

1900 *Equisetites columnaris* (Brongn.): Seward, in part, p. 53, pl. 19, figs. 1–3 only. (Erect stems; fig. 3 is inverted.)

1913a *Equisetites columnaris* (Brongn.): Halle, p. 3, pl. 2. (Discussion of stems in position of growth.)

1941 *Equisetites columnaris* (Brongn.): Harris, p. 292, text-figs. 1, 2. (Stem, node and sporangiophore.)

1945 *Equisetites columnaris* (Brongn.): Harris, p. 227, text-fig. 7. (Details of node.)

2. Specimens from various regions doubtfully determined or distinct:

1900 *Equisetites columnaris* (Brongn.): Seward, in part, pl. 19, figs. 4, 5 only; text-figs. 3, 4. (*E. laterale*; Yorkshire.)

1907 *Equisetites* cf. *columnaris* (Brongn.): Seward, p. 3, pl. 1, figs. 1, 2. (Imperfect Russian specimen, probably upside down.)

1907 *Equisetites columnaris* (Brongn.): Stopes, p. 378, pl. 27, fig. 1. (Leaf teeth of *E. laterale*, Brora, Scotland.)

1909 *Equisetites* cf. *columnaris* (Brongn.): Salfeld, p. 8, pl. 2, figs. 2, 5–7. (See p. 16.)

EMENDED DIAGNOSIS. Rhizome horizontal with short internodes, bearing erect stems terminally or laterally and long vertical roots 5 mm. wide and more slender horizontal roots.

Erect vegetative stem unbranched, typically 4–5 cm. wide below (rarely 6.5 cm. wide) probably very tall. Lower nodes rather crowded, upper ones at 5–15 cm.; lower nodes often bearing 4–6 bulges (? arrested buds), and occasionally a few roots; upper nodes without bulges; stem probably tapering upwards to about 2 cm., but sometimes ending in a large conical bud. Nodes usually slightly swollen but sometimes equalling the internode, never constricted.

Internode smooth, without internal or external ribs or angles. Stomata absent from lower parts of stem, but numerous and evenly scattered over the internode and leaf sheath of the upper parts, forming distinct pits, rest of epidermis formed by uniform, slightly bulging cells. Cuticle thin, stoma typically about $70\mu \times 40\mu$, not ornamented, pit wide and shallow, epidermal cells typically about $60\mu \times 30\mu$, outlines very ill-marked but ends and sometimes sides of

cells conspicuously puckered. Surface of cuticle without rings; sometimes cell surface showing distinct longitudinal striations and cell ends and sides marked by conspicuous thickened dots. Cells in region of commissural furrows of leaf sheath with coarsely sinuous lateral walls.

Leaf sheaths with 50–80 segments in the lower part of the stem, number reduced to about 25 on the upper nodes. Sheath on lower nodes typically 2 cm. long (but commissural furrows continued for 1–2 cm. below the node) composed of raised leaf segments and sunken commissural flanges; flanges truncate above, the two flanges together slightly broader than the leaf segments at the top of the sheath but tapering evenly to a point downwards. Free leaf teeth diverging somewhat from the stem, usually 4 mm. long, acute (range 2–5 mm.). Leaf sheaths of upper nodes similar to lower ones but smaller in all their parts.

Nodal diaphragm rather thick, but fragile particularly in the larger stems, firmly attached and not rotating on compression, surface finely granular, showing a single ring of tubercles about 5 mm. from the edge, tubercles twice as numerous as leaf teeth (? = nodal metaxylem masses). Cones and fertile stems not known in attachment (for description see below).

HOLOTYPE. Paris Museum (Figured Brongniart, 1828, pl. 13).

DISTRIBUTION. *E. columnare* is abundant throughout the Lower and Middle Deltaic Series where it is by far the commonest recognisable fossil. Cuticle fragments agreeing with it are to be found in over half the successful macerations of rock in bulk and many of the coal seams seem to be composed of this one species. If the beds of truncated roots belong to it, as they well may, its abundance is even more remarkable and it would be fair to describe the Lower and Middle Deltaics as a swamp largely covered by *E. columnare* but in which other plants are locally common.

For some reason erect stems of *E. columnare* in the position of growth (see Halle, 1913a), occur in the Lower Deltaic Series only, but broken and flattened stems are equally abundant at all levels. No specimen has been found in the Upper Deltaic Series; *Equisetum* cuticle fragments are relatively rare in the Upper Deltaic Series and those found, though matching *E. columnare* reasonably well, have not been determined because they might equally well belong to *E. beani*, the cuticle of which is unknown.

E. columnare is scarcely known outside Yorkshire. The specimens from Brora in Sutherland, Scotland in rocks of about the same age are probably identical (but there is possible confusion about the origin of some of the figured specimens). The specimens from other countries mentioned below are not accepted as reliably determined.

'*Equisetites* cf. *columnaris*' of Salfeld (1909) from the Upper Lias of N. Germany is in my opinion distinct. One specimen (fig. 2) shows commissures which die away well above the node; figs. 6 and 7 show very narrow leaf teeth of different form; fig. 5, which to judge by the short internodes is a stem base, is only 2 cm. wide and is outside the ordinary range of *E. columnare* stem bases. Salfeld's pl. 2, fig. 3 (*E.* cf. *muensteri*) is actually closer to *E. columnare* than the above.

Hirmer (1927: 460) states that the species occurs in the Keuper of S. Germany and the Alps and in the Jurassic of China, but I have not seen any evidence of this distribution.

DISCUSSION. Nearly all the figured specimens of *E. columnare* and nearly all the Museum specimens are erect stem bases preserved in the position of growth. Such specimens are common in the field (I have found them in fifteen localities), but compressions of stem and

leaf sheath fragments are far more abundant and have been seen in two or three hundred localities. They are so widespread I have not troubled to record them, but they are certainly the commonest recognisable fossils in the Deltaic Series. Vertical roots probably belonging to this species are commoner still.

Winch (1821) makes the following reference to this species, the earliest traced: 'Gigantic reeds resembling *arundo donax* are found in the sea cliffs opposite High Whitby. They appear to have been rooted in a bed of shale or slate-clay, and their remains protrude into a stratum of sand-stone five feet thick. Those which stand erect retain their shape, but those which do not are compressed. Their tops seem to have been broken off; the woody matter has disappeared, leaving sand-stone casts. Casts of *Euphorbiae* are also found in the sand-stone strata above the alum rocks. Wood mineralised by iron is frequently found at Kettleness and Stowbrow. Trunks and branches of fossil trees, the bark and softer parts of which have been changed into jet, are frequently met with in the alum shale: and leaves and impressions like those of the palm, are found in the sand-stone and iron-stone.'

Young & Bird (1822) noticed the relation of the erect stems to the underlying coaly layer and vertical roots, but it is seldom easy to trace either the stem or root into the horizontal rhizome, which is crushed, having no filling with rock. Any relation is lost when the specimen of an erect stem cast is collected and Seward, working with Museum material, suggested that they had drifted and sunk before being preserved in a vertical position. Halle (1913*a*), however, gave convincing evidence that they are truly in the position of growth, and I have seen many similar but less good specimens.

The erect stems are gregarious (occurring 10–20 cm. apart) and are always broken off, usually all at the same level 50–100 cm. from the base. One imagines them growing as a pure stand in a pool, rooted in the peaty silt beneath. Suddenly the pool was overwhelmed with coarse sandy silt; the stems died, the tops broke off and silt filled them through breaks in the nodal diaphragms; the peaty matter round the rhizomes forms a little coal seam and the roots remain in the silt beneath. Where no such early catastrophe occurred the peaty matter (composed almost entirely of the broken stems) accumulated to form a coal seam 10–20 cm. thick; but where a wandering stream cut away the whole of the land surface, and this is the commonest case, nothing remains but the vertical roots.

Many of the erect stems show 3–6 conspicuous bulging swellings at the nodes. These swellings are most frequent on the larger stems (such as most authors have figured) and are usually absent on the smaller ones. Seward (1900) considered that they represented branch scars. I think however that the breaks in the leaf-sheath shown in his pl. 19, fig. 1 occurred when the specimen was collected. In similar specimens still in the matrix there are no branches running out from the bulges, though there may occasionally be a small horizontal root. In most sheaths there is no break at all, and I regard them as dormant buds under the sheath, possibly fertile buds. In a few favourable specimens the bulges appear to alternate with leaves, but as a rule the relation is unknown.

These bulges form a rather regular pattern, alternating at successive nodes, though without perfect regularity. Some examples are given below:

In the Geology Department of Leeds University, there is an erect stem, 30 cm. \times 6.2 cm., showing a contracted base and nine nodes, all but the lowest bearing about five swellings in rather regular alternation.

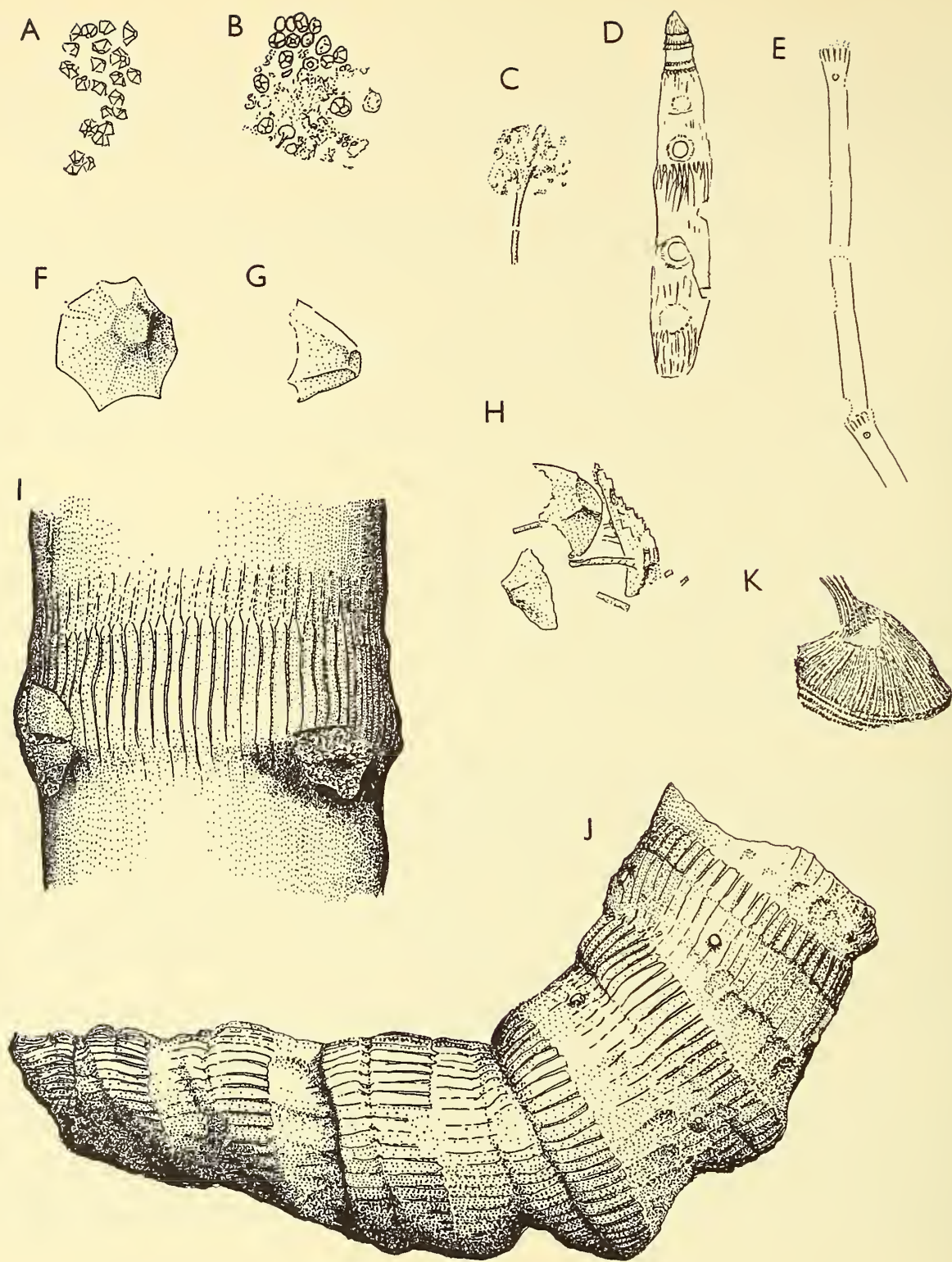


Fig. 4. *Equisetum columnare* Brongniart

A, cone fragment, V.30919, $\times 1$. B, cone fragment, V.30922, $\times 1$. C, sporangiophore stalk, V.30920, $\times 5$. D, slender stem showing three leaf caps and four rotated nodal diaphragms, V.30924, $\times 1$. E, slender stem (the lowest node, not shown, is 7.5 cm. below the middle one). Note small rotated diaphragms, V.30923, $\times 1$. F, G, sporangiophore heads, V.30919, $\times 5$. H, fragment of cone axis and displaced sporangiophores, V.30921, $\times 5$. I, large erect stem showing two broken nodal bulges; on the left some of the internode and diaphragm are exposed. The free leaves are unusual in being pressed against the stem, V.28538, $\times 1$. J, crushed rhizome in side view passing into base of erect stem; the upper nodes show small bulges perhaps root scars; the diaphragms of the lowest nodes show oblique displacement, V.8972, $\times 1$. K, rhizome bud showing three nodes and converging leaves, V.31321, $\times 1$.

A-H, Beast Cliff, Petard Point; I, Arncliffe, Osmotherly; J, Yorkshire (exact locality unknown); K, Roseberry Topping.

In one Yorkshire Museum specimen No. 714, a stem 6.5 cm. wide with 3 nodes, the arrangement is as follows. (A, B, C, D represent the nodal swellings of successive nodes and the numbers represent the number of leaf teeth between swellings.)

$$\begin{array}{c} A - 25 - B - 13 - C - 26 - D - 18 - A \\ \quad A - 39 - B - 24 - C - 26 - A \\ A - 24 - B - 15 - C - 24 - D - 28 - A \end{array}$$

Other specimens in the Yorkshire Museum are as follows: A stem (with no number) base 20 cm. long, 4 cm. wide with 12 nodes. Each node has 6 or 7 swellings but some are very obscure. The better marked swellings at least, alternate regularly.

In a second Yorkshire Museum specimen (also numbered 714) a stem 12 cm. long and 6.5 cm. wide, with three nodes, the top node has four swellings of which two are small and close together, the middle node has three swellings and the bottom node has four, of which two are again small and close together. Here the two small, closely placed swellings behave as one in the alternation.

It is interesting that no stem shows any sign of ribs on the cast or of longitudinal strands of coaly matter such as would be left by woody bundles. The tissue of the stems seems to have been rather unsubstantial. At the very base of the erect stem, however, where it tapers as it joins the side of a rhizome, the substance becomes a good deal thicker, but even here there are no woody strands. *E. columnare* probably had a carinal canal rather than a tracheidal conducting system.

Some slender stems 4-9 mm. wide which are thought to be fertile stems of *E. columnare* are attributed to it mainly on the basis of their association in four localities where *E. columnare* occurs in abundance without other species. They agree with it in the general form of the leaf sheath but the free teeth, 15-20 in all, are directed upwards. The diaphragms show marginal tubercles and a granular centre and are similar in general structure to those of the smaller normal stems of *E. columnare* (and differ greatly from those of *E. laterale*), but they are unusual in having rotated on compression, a phenomenon which does not occur in ordinary stems of *E. columnare*. The stem substance is delicate and the cuticle was not successfully prepared.

The specimen shown in Text-fig. 4 D is of special interest in that it is unexpanded. The pointed apex is formed by three overlapping caps and seems to consist of entire leaf sheaths which have torn away from their nodes, and a little below the bare nodes are seen. Again the diaphragms have rotated.

These slender stems are of problematical nature; the possibility is not excluded that they represent an otherwise unknown species of the Yorkshire flora (closely resembling the Rhaeto-Liassic *E. muensteri*). If they do belong to *E. columnare*, they may be fertile shoots, but they may equally well be slender stems produced under special conditions.

The specimen shown in Text-fig. 4 K is regarded as a rhizome apex. It shows three swollen nodes from which numerous slender leaves arise and converge to a point. Layers of mud occur between the leaf-sheaths and a good deal of mud occupies the interior. Rather similar specimens have been seen at the Beast Cliff *Equisetum* Bed and seem particularly common at Roseberry Topping. The collection of Dr. H. H. Thomas includes many specimens which appear intermediate between this and the small stem shown in Text-fig. 4 D.

The cones attributed to *E. columnare* are expanded and a good deal broken; there are also a few isolated sporangiophore heads. These isolated specimens were attributed to the stems on the evidence of association, they have been found with the stems at five different localities in none of which are other Equisetales known.

In these cones the axis is very delicate and about 3 mm. thick. It shows no details, but the sporangiophores have robust heads about 3 mm. wide and rather long stalks. The head shows a concave central area and about six depressed sides, a few stomata have been observed on the outer epidermis. The inner surface shows faint ridges radiating from the stalk. No sporangia remain, nor, therefore, are the spores known.

Celloidin pulls were made from certain cones from the Beast Cliff *Equisetum* Bed. Various spores are present; by far the commonest is a small, oval, smooth-walled kind about $15\mu \times 13\mu$. They are very unlike Recent *Equisetum* spores and it is not suggested that they belong to *E. columnare*.

COMPARISON. Seward's (1900) account of *E. columnare* is clouded by two mistakes: several of the specimens were described upside down, as they were in other species also, and *E. laterale* was united to *E. columnare*. Both mistakes are easy in dealing with Museum collections; it is of course then impossible to see the position of the erect stem in the rock; and the fact that *E. columnare* and *E. laterale* do not intergrade in the field is not obvious in mixed collections. Seward's diagnosis (1900) refers to both species.

E. columnare in its typical form is easily distinguished from nearly all other species, but *E. mytharum* Heer (redescribed by Ricour, 1948) is very similar particularly in the cellular sculpture of the leaf-sheath. It is distinguishable, however, by its more crowded nodes and somewhat broader commissures.

For differences between *E. columnare* and other Yorkshire species see pp. 14-15.

FUTURE WORK. Although *Equisetum columnare* must be among the best known species of the genus it is not yet known how the cones are born. The bulges on the lower nodes of the erect stem might represent dormant cone buds, which would presently emerge on special slender stems, but I found no evidence at all of this and from their rarity it is clear that the cones were seldom produced, or at least rarely preserved. If this were cleared up by some fortunate specimen it would be possible to make a complete restoration of *E. columnare*.

Equisetum laterale Phillips

Text-figs. 5 A-D, G, H; 10 A

1. Yorkshire specimens.

- 1829 *Equisetum laterale* Phillips, p. 153, pl. 10, fig. 13. (Sketch of stem and diaphragm.)
- 1836 *Equisetum laterale* Phillips: Lindley & Hutton, p. 95, pl. 186. (Stem and diaphragm.)
- 1851 *Asterophyllites? lateralis* (Phillips) Bunbury, p. 189. (Description.)
- 1856 *Calamites lateralis* (Phillips) Zigno, p. 46, pl. 3, fig. 3. (Leafy stem.)
- 1875 *Equisetites lateralis* (Phillips) Phillips, p. 196, pl. 10, fig. 13. (Figure as in 1829.)
- 1898 *Equisetites lateralis* (Phillips): Seward, p. 275, text-figs. 58 F, 63, 64. (Leaf sheath, stem and diaphragm; figs. 63, 64a are upside down.)
- 1900 *Equisetites columnaris* (Brongn.): Seward, in part, pl. 19, figs. 4, 5; text-figs. 3, 4 (as in 1898, text-figs. 63, 64). Text-fig. 3 is the specimen described by Bunbury (1851) and by Zigno (1856). Pl. 19, fig. 5 is from Leckenby Coll., Sedgwick Museum, Cambridge. Other specimens are *E. columnare*.
- 1945 *Equisetites lateralis* (Phillips): Harris, p. 222, text-figs. 3, 5, 6. (Stem, cuticle.)

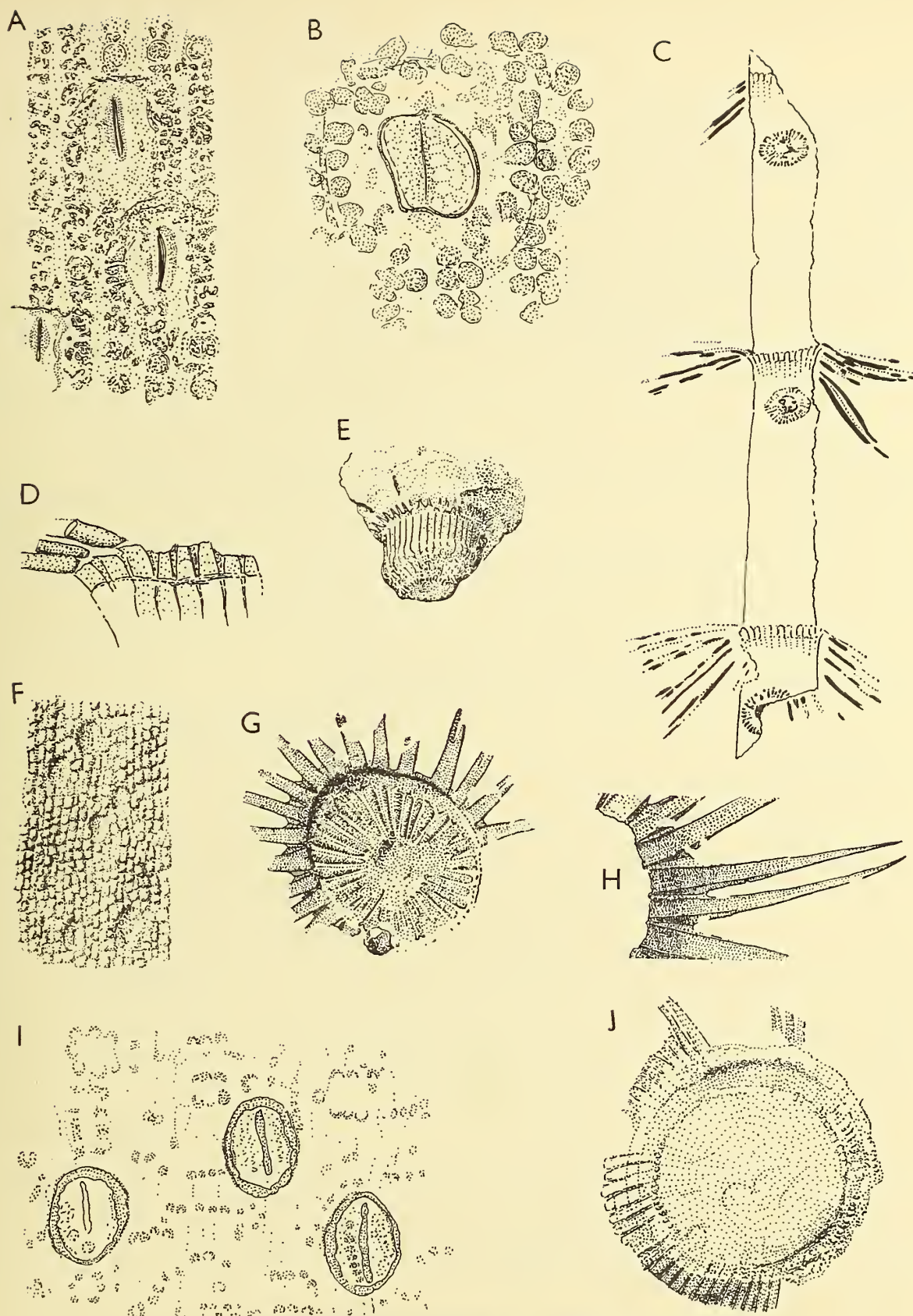


Fig. 5. *Equisetum laterale* Phillips, *E. columnare* Brongniart

A, *E. laterale* cuticle, Gripe Howe, V.34308, $\times 200$. B, *E. laterale* cuticle, Whitby Long Bight, V.34309, $\times 400$. C, *E. laterale* specimen 40561 redrawn, $\times 1$. D, details of middle node of C. E, *E. columnare* small nodal diaphragm and leaf sheath, Leckenby Coll. no. 25, Sedgwick Museum, Cambridge, $\times 1$. F, *E. columnare* surface markings of internode, Gristhorpe Bed, V.26789, $\times 40$. G, *E. laterale* diaphragm and leaf whorl, ? Haiburn Wyke, V.26892, $\times 2$. H, *E. laterale* typical leaf teeth, ? Haiburn Wyke, V.26893, $\times 4$. I, *E. columnare* cuticle of internode, Hasty Bank, V.34311, $\times 200$. J, *E. columnare* large nodal diaphragm, Roseberry Topping, V.31043, $\times 1$.

The cuticles are drawn under phase-contrast illumination. E, G, H, are from Harris (1945); F from Harris (1941).

2. Specimens from Scotland.

- 1907 *Equisetites columnaris* (Brongn.): Stopes, p. 378, pl. 27, fig. 1. (Leaf teeth.)
 1907 *Equisetites broaensis* Stopes, p. 379, pl. 27, fig. 2. (Isolated nodal diaphragms.)

3. Other specimens closely comparable with *E. laterale*.

- 1880 *Equisetum lakusenii* Romanowski, p. 127, pl. 24, figs. 1, 2. (Good stems and diaphragms. Central Asia.)
 1883 *Equisetum rotiferum* Tenison-Woods, p. 66, pl. 6, figs. 5, 6. (Australia.)
 1907 *Equisetites ferganensis* Seward, p. 17, pl. 2, figs. 25-28, ?29. (Chinese Turkestan.) Not pl. 2, figs. 30, 31 nor pl. 3, figs. A, H, J which seem to be *Neocalamites*.
 1911 *Equisetites ferganensis* Sew.: Seward, p. 35, pl. 1, figs. 5-8. (Chinese Dzungaria.) Not pl. 1, figs. 1-4, 9, 10 which seem to be *Neocalamites*
 ?1911 *Equisetites ferganensis* Sew.: Seward & Thomas, p. 18, pl. 2, fig. 9, or possibly *Neocalamites*. (Irkutsk).
 1912 *Equisetites ferganensis* Sew.: Seward, p. 4, pl. 1, figs. 2-14, 19, ?15-18. (Afghanistan.) Not fig. 1 (?*Neocalamites*).
 1915 *Equisetum rotiferum* Ten.-Woods: Walkom, p. 27, pl. 1, figs. 2, ?3; pl. 2, fig. 4. (Australia.)
 1917 *Equisetites nicoli* Arber, p. 26, pl. 3, fig. 2. (Stems and nodal diaphragms. New Zealand.)
 1925 *Schizoneura lateralis* (Phillips) Teilhard de Chardin & Fritel, p. 538, pl. 23, figs. 3, 4. (Good diaphragms. S. China.)
 1930 *Equisetites ferganensis* Sew.: Turutanova-Ketova, p. 132, pl. 1, fig. 13; p. 141, text-fig. 25. (Central Asia.)
 1931 *Equisetites* cf. *lateralis* (Phillips): Sze, p. 51, pl. 5, fig. 4. (China.)
 1931 *Equisetites ferganensis* Sew.: Prinada, p. 20, pl. 1, figs. 1, 2. (Central Asia.)
 1933 *Equisetites ferganensis* Sew.: Kryshstofovich, pl. 3, fig. 5. (Baikal.) Not pl. 5, fig. 5 nor pl. 10, fig. 1 which appear to be *Neocalamites*.
 1933 *Equisetites* sp., Yabe & Oishi, p. 202, pl. 30, figs. 1-3. (Manchuria.)
 1933b *Equisetites* cf. *lateralis* (Phillips): Sze, p. 69, pl. 9, fig. 7. (China.)
 1934 *Equisetites nicoli* Arber: Edwards, p. 90, pl. 4, fig. 3. (New Zealand.)
 1937 *Equisetites longifolia* Brick: Brick, p. 48, pl. 14, fig. 1. (Isolated leaf whorl. Central Asia.)
 ?1937 *Equisetites ferganensis* Sew.: Brick, p. 46, pl. 13, figs. 1, 2. (Similar size but neither free leaves nor diaphragm. Central Asia.)
 1938 *Equisetites ferganensis* Sew.: Prinada, pl. 5, figs. 3-7.
 ?1949 *Equisetites* cf. *sarrani* Zeiller: Sze, p. 3, pl. 15, figs. 1-3, also possibly figs. 4, 5. (Stem and diaphragm. Hupeh, China.)
 ?1952 *Equisetites* cf. *sarrani* Zeiller: Sze & Lee, pp. 2, 20, pl. 1, figs. 1-5. (Stem and diaphragm. Szechuan, China.)
 1956 *Equisetites lateralis* (Phillips): Semaka, p. 107, text-figs. 1, 10. (Diaphragm. Lias; Roumania.)

EMENDED DIAGNOSIS. Erect vegetative stems unbranched, typically 1.5 cm. wide (1-3 cm.), internodes typically 3 cm. long (up to 6 cm.); apex of stem often formed by a large conical bud. Nodes not swollen, not externally marked. Internodes usually smooth externally or with very obscure angles below the leaves; internally showing no sign of woody bundles. Surface showing the raised margins of uniform epidermal cells; stomata evenly scattered on certain internodes and lower parts of leaf sheath (absent from leaf teeth and from some parts of the stem), guard cells superficial. Cuticle of internode thin; showing rows of uniform, rectangular epidermal cells typically about $50\mu \times 30\mu$ and scattered oval stomata typically $50\mu \times 35\mu$. Cell outlines very ill-marked, but interior of each epidermal cell often marked by a ring of curved thickenings, occasionally amounting to a ring of small solid papillae or of rings. Guard cell outlines distinctly marked, surface wall thin, faintly pitted. Cells around the stomata somewhat sunken and with slightly thinner surface walls. Cells of commissural flanges of leaf sheath elongated, with well-marked sinuous walls.

Leaf sheath 1-2 cm. long, often somewhat enlarged above, lower part not distinguishable from internode, upper half divided into 25-35 leaf tooth segments separated by sunken commissural flanges. Leaf segments at the top of the sheath rather broader than the adjacent pairs

of flanges, flanges truncate above, tapering to a point at about halfway to the level of the nodal diaphragm.

Free leaf teeth straight, typically 10–15 mm. long, diverging from the stem, substance thick, midrib present, surface cells elongated, stomata absent. Marginal cells projecting as minute teeth.

Nodal diaphragm robust, nearly round, concave above, loosely attached and usually rotating on compression, width about two-thirds of width of stem. Diaphragm composed of firm and of delicate tissue. Firm tissue forming a wheel consisting of a hub, spokes and a rim; delicate tissue (usually lost) occupying the hole in the hub and the intervals between the spokes. Number of spokes equal to number of leaves; length of spoke usually half or two-thirds of total radius of diaphragm. Cone unknown.

HOLOTYPE. Specimen figured Phillips (1829, pl. 10, fig. 13); ?Yorkshire Museum.

DISTRIBUTION. Lower Deltaic (four localities) and Middle Deltaic (Gristhorpe Series, six localities and Sycharham Series, one locality) of Yorkshire. It may be commoner than this as cuticle fragments which may belong to it have not been recorded. Inferior Oolite of Brora, Scotland. Specimens of roughly similar age are widespread in Asia.

DISCUSSION. *E. laterale* is represented by many specimens and where it occurs it is often the only species and overwhelmingly abundant, evidently forming a pure stand. The specimens are all compressed fragments of erect stems; there are no rhizomes nor casts of erect stem bases. No cone or fertile shoot is known and the little cap-shaped organs noted in association with it (Harris, 1945: 227) are still not understood. They have been found again, but only in the original bed in the Cloughton Wyke Cliffs.

As far as I know the wheel-like diaphragm of *E. laterale* does not occur in Recent species and it would be interesting to understand its structure better. It is clear that the spokes equal the leaves in number and it is probable that they alternate with them (Text-fig. 5 G).

The specimen (40561) figured by Zigno (1856, pl. 3, fig. 3) and by Seward (1900, text-fig. 3) appeared anomalous and has been redrawn. It is less unusual than was suggested by the figures, which were upside down. The diaphragms are at their usual level about 1 cm. below the top of the leaf sheath, and the leaves (not stem branches) are only about 1.5 cm. long, not 2.5 cm. long. The detached pieces of leaf which suggested the greater leaf length, belong to an adjacent stem. It does show one unusual feature, the leaves are distinctly reflexed at the point where they separate from the leaf sheath; and it is unusual in preservation in that the free leaves have been impregnated with iron and are solid rods. The diaphragms are rather oval and somewhat damaged, but appear to have rather large hubs and about 32 spokes. The exposed surface of the leaf sheath shows about 15 segments so no doubt there were in all as many as the spokes.

Seward included in his *Equisetites ferganensis* a number of specimens showing striated internodes as in *Neocalamites*, believing them to represent the stele of *E. ferganensis*. No specimen, however, shows such a striated core in conjunction with the external features of *E. ferganensis* and these specimens are excluded. In no Yorkshire specimen is there any suggestion of a *Neocalamites*-like stele.

The cuticle of *E. laterale* is delicate and hard to prepare and the preparations only show the cell outlines obscurely. They are much clearer under phase-contrast lighting, when the surface pitting (presumably related to original silica granules) is visible.

COMPARISON. *E. laterale* has suffered eclipse; it was recognised until 1900 and then merged into *E. columnaris*; but in effect revived under the new name *E. ferganensis* (Seward, 1907) without relation to its earlier history. Further study alone can settle whether any of the material called *E. ferganensis* is to be regarded as distinct, some is indistinguishable on present evidence. *E. laterale* is distinguished from *E. columnare* on p. 14.

E. laterale is a member of the group which have small stems and wheel-like diaphragms. This group includes the specimens cited under the names *E. laterale* and *E. ferganensis* in which the leaves diverge and so are often broken off. There are a few other species in which the leaves are appressed to the stem and thus well distinguished, including *E. blandum* Raciborski (1894), *E. möbergi* Möller (see Halle 1908; Möller & Halle, 1913) and *E. grosphodon* Harris (1931).

In the *E. laterale* subgroup, with spreading leaves (see synonymy) though the specimens agree closely there does seem to be some variety, for instance a few of the Asiatic specimens have distinctly oval instead of round diaphragms; and others have a rather larger hub and consequently shorter spokes. Some too are larger than any Yorkshire specimen seen. These characters vary independently and although certain Asiatic specimens fall outside the range of variation of the Yorkshire material, it is difficult to separate them specifically. They need further investigation.

Fox-Strangways & Barrow (1892: 127) included *E. laterale* in *Phyllothea* for it much resembles *P. australis* in its sheaths and leaves. It is here returned in *Equisetum* chiefly for custom, and because the differences between its leaves and those of *E. columnare* are also slight. Its diaphragms seem nearer those of certain more normal *Equisetum* species (*E. blandum*, *E. möbergi*, *E. grosphodon*) mentioned above than anything known in *Phyllothea*. The cone, which might settle this, is unknown.

Phyllothea sibirica Heer (1876a; 1878) is very like *E. laterale* indeed but has rather narrow stems. It scarcely helps because its position is also doubtful.

Equisetum beani (Bunbury) n. comb.

Text-fig. 6 A, B

1. Yorkshire specimens.

- 1851 *Calamites beani* Bunbury, p. 189.
- 1856 *Calamites beani* Bunbury: Zigno, p. 45, pl. 3, fig. 1. (Good figure.)
- 1886 '*Calamites beani* Bunbury': Gardner, p. 201, pl. 9, fig. 3. (Brief description as potential fossil Monocotyledon.)
- 1898 *Equisetites beani* (Bunbury) Seward, p. 270, text-figs. 60-62. (Fig. 60 from Gardner, 1886; figs. 61 and 62 are probably upside down.)
- 1900 *Equisetites beani* (Bunbury): Seward, p. 63, text-figs. 5, 6. (As figs. 60, 61 above.)

2. Specimens of similar appearance from other regions.

- 1908 *Equisetites* cf. *beani* (Bunbury): Halle, p. 20, pl. 5, figs. 1-8. (Lower Lias; Sweden.)
- 1911 *Equisetites beani* (Bunbury): Thomas, p. 57, pl. 1, figs. 3, 4. (Figures upside down. Russia.)
- ?1911 *Equisetites halleri* Thomas, p. 58, pl. 1, figs. 5-7. (All smaller than typical Yorkshire specimens. Russia.)
- 1937 *Equisetites beani* (Bunbury): Brick, p. 49, pl. 14, fig. 2. (Defoliated stem, upside down. Central Asia.)

EMENDED DIAGNOSIS. Rhizomes and stem bases typically 10-12 cm. broad, with internodes only 3-5 cm. long; aerial stems arising from a constricted base, but becoming 10-12 cm.

broad (sometimes smaller) with internodes 10–15 cm. long. Nodes of rhizomes and of aerial stems showing a slightly constricted band, 2–3 mm. wide, at the nodal diaphragm. Surface of upper part of internode divided by shallow commissural furrows into the decurrent bases of about 100–150 segments up to 2 mm. wide, furrows dying away 1–2 cm. below the node (free part of leaf sheath and leaf teeth not known). Interior of internode showing fine woody strands at intervals of 0.75–1 mm. (being twice as numerous as the leaf furrows of the same specimen). Nodal diaphragm circular, robust, surface smooth except at the extreme edge where it is marked with fine ridges or elongated tubercles, twice as numerous as the leaves. Cuticle not known. Cones unknown.

HOLOTYPE. Specimen no. 88 in the Manchester Museum.

DISTRIBUTION. *Equisetum beani* is recorded from twelve localities and Museum specimens certainly represent additional localities. Eight of the recorded localities belong to the Upper Deltaic where it is locally common, especially in the cliffs near Scarborough, and is the only known member of the Equisetales. It extends throughout the whole Deltaic Series, being known from two localities in the Lower Deltaic; and one in each division of the Middle Deltaic. Wherever it occurs at all it is to be found in some abundance, but no specimen has yet been seen in the position of growth, nor has it been possible to relate any of the Upper Deltaic root beds to this species.

DISCUSSION. *E. beani* is locally abundant but no specimen yet found is perfect; it must have lost its leaf sheath very easily and with this its most important characters. Many specimens, however, show furrows dying away below the node. One is figured upside down by Seward (1898, text-fig. 61; 1900, text-fig. 6). A few specimens show in addition large but ill-defined longitudinal depressions, 5 mm. broad, running most of the length of the internode, probably caused by crushing. Many specimens also show coaly ridges or strands running the whole length of the internode without dying away at all; these are represented by Seward (1898, text-fig. 61, near the top and text-fig. 62 throughout, both figures being inverted). Such strands occur at intervals of about 0.75 mm. in some specimens and just over 1 mm. in others.

These coaly strands probably represent woody strands in the original stem and where a specimen shows both these and leaf base furrows they are just twice as many as the leaves. I have previously discussed such strands in fossil *Equisetum* stems (Harris, 1937: 7) reaching the conclusion that they may not represent whole bundles but only the two metaxylem strands of a single bundle.

COMPARISON. *E. beani* is incompletely characterised; and as its leaf sheath is not known it cannot be fully compared with other species and indeed there is no proof that it is rightly placed in *Equisetum*. The field evidence shows that it is distinct from *E. columnare* (the two are not found together). It is distinguished from defoliated stems of *E. columnare* by its greater diameter (though the size ranges of the two species overlap), by its woody vascular strands (not however always shown) and by its constricted node and more robust diaphragm (again not always seen).

E. beani is a good deal larger than any other Jurassic species but in the Trias there are several at least as large, in particular the Keuper species *E. arenaceus* which looks very similar when defoliated. *E. arenaceus* appears to differ in its elaborately sculptured diaphragm, though this is not quite clear since two kinds of diaphragms have been attributed to it (see Frentzen, 1933).

Equisetum sp. A.

Text-fig. 6 C-H

DESCRIPTION. Stem (known from small fragments only), typically 2 mm. wide, extremes 1 and 4 mm., manner of branching not known. Internodes relatively long, nodes not enlarged (base of internode contracted), leaf sheath short, divided into leaf segments and sunken commissures, commissures not extending below the node. Free leaves not known. Internode showing up to 8 low ribs continuing the leaf segments downwards.

Cuticle rather thick (1μ – 3μ) and robust. Epidermal cells of internode almost uniform short rectangles forming perfect longitudinal rows; stomata occurring on the leaf segments of the sheath and in the grooves on the internode. Lateral walls of epidermal cells appearing broad and straight and moderately well marked, showing at high magnification a finely sinuous thickening. End walls less well marked, often composed of about three thickenings side by side. Epidermal cells of the commissures of the leaf sheath with coarsely sinuous and sharply marked walls. Surface walls of internodal epidermal cells showing about 1–4 ill-defined longitudinal ridges; surface of cells of internodal ribs more thickly cutinised but otherwise like those of the grooves.

Stomata usually widespread in the broad internodal grooves but sometimes rare or absent; forming short longitudinal files of about six separated by one or two ordinary cells and separated laterally from other files by at least one row of ordinary cells. Guard cells sunken to form a shallow pit, cuticle often folded at the sides of the pit, but not markedly overhanging. Surrounding epidermal cells forming a shallow pit with vertical sides, occasionally surface of epidermal cells showing furrows radiating from the stoma, but otherwise unspecialised. Stoma small, circular or slightly elongated transversely. Guard cell cuticle flat, rather thin, showing two or three rows of small pits. Aperture longitudinal, well marked. Leaf sheath without stomata, cuticle becoming delicate above.

Trichome bases sometimes frequent, either evenly scattered or arranged in short longitudinal files, consisting of an indistinct rounded print situated over the middle of a cell or over its end wall.

DISCUSSION AND OCCURRENCE. *Equisetum* sp. A. is known from very numerous fragments of cuticle, none over a centimetre long, obtained by macerating certain shales and coals in bulk. No intact specimen has yet been seen. It has been noted in fifteen localities scattered over the whole outcrop and ranges throughout the Lower and Middle Deltaic Series. It is sometimes present in masses, for example, at the tip heaps of the coal pits of Stonymoor, Snilesworth, and being virtually the only species found in the macerations may have contributed largely to the formation of that particular coal.

Equisetum sp. A. has not been described as a new species because its gross form is unknown. As it is fairly common it is reasonable to hope that specimens showing the form will be found. It differs from nearly all the Mesozoic species in its very slender stems and is indeed more slender than most of the Recent species. It agrees, however, with the Korean *Equisetites nakdongensis* Tateiwa (see Oishi, 1940) in the width of the stem and number of leaf teeth and may indeed be identical with it but further information is needed. *E. nakdongensis* occurs in beds correlated with the Upper Jurassic and Lowest Cretaceous and is therefore younger than *Equisetum* sp. A. *Equisetites scitulus* Frenguelli (1943) is another slender plant of Mesozoic Age.

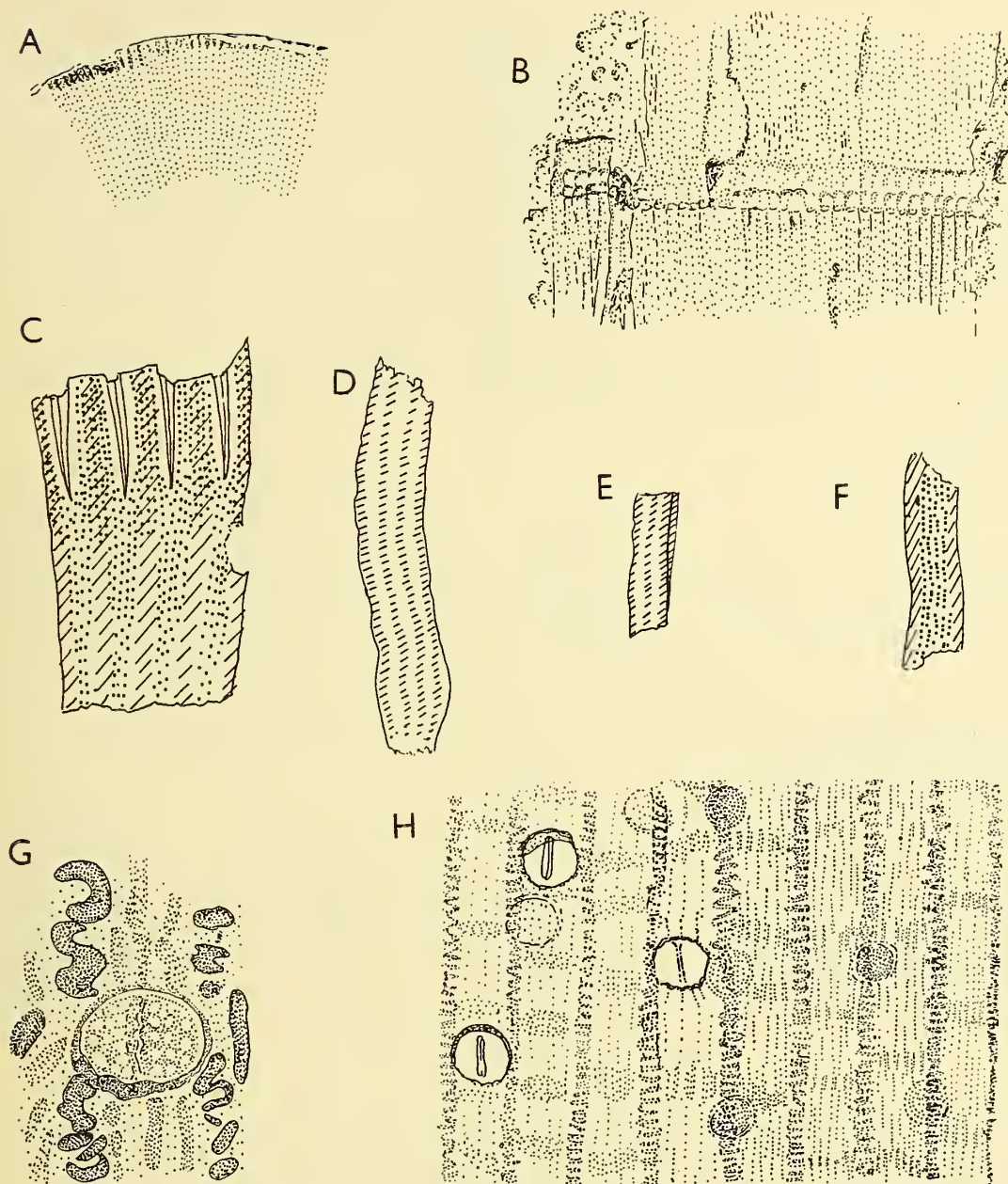


Fig. 6. *Equisetum beani* (Bunbury), *Equisetum* sp. A

A, B, *Equisetum beani*. A, edge of a nodal diaphragm 10 cm. wide, Beast Cliff *Zamites* Bed, V.30934, $\times 1$. B, node of aerial stem (internode exceeds 14 cm. in length), Jugger Howe Beck, V.30935, $\times 1$.

C–H, *Equisetum* sp. A. C, fairly large stem and leaf sheath showing the distribution of stomata (dotted) and thicker cells (ruled). The stomata are not represented individually. Fallen block, Widdy Head, V.34312, $\times 8$. D, internode (without stomata), there are probably eight ribs of which the upper four are shown (ruled). Stonymoor Beck Coal pit, V.34313, $\times 8$. E, internode of small stem with about five ribs in all, stomata present but omitted. Stonymoor Beck Coal pit, V.34314, $\times 8$. F, internode with only two ribs and two stomatal bands (upper one stippled) Fallen block, Widdy Head, V.34315, $\times 8$. G, details of stoma, V.34315, $\times 400$. H, cuticle showing three stomata and seven trichome bases. V.34315, $\times 200$.

Other Yorkshire species of *Equisetum*

All the hand-specimens I have seen and almost all the cuticle fragments obtained from macerations of shales and coals can be identified with forms described here or dismissed as ill-preserved. There are only two other types of cuticle which seem to belong to *Equisetum*, but cannot be matched. One of these '*Equisetum* sp. B.' which occurs in four Middle and Lower Deltaic shales has an internode cuticle rather like that of *E. columnare* but the stomata are deeply sunken in conical pits. The other, '*Equisetum* sp. C.', which is only known from the Gristhorpe Bed is also rather like *E. columnare*, but the stomata are larger ($150\mu \times 100\mu$) and more obviously pitted. Neither seems worthy of description.

The fewness of these undetermined Equisetales suggests that this family, as it grew in the Yorkshire Jurassic, is relatively well represented by the known fossil species. The position is widely different for several other families.

Genus NEOCALAMITES Halle, 1908:6

Neocalamites is a Mesozoic genus of large *Calamite*-like stems and leafy shoots. Halle's diagnosis cannot be improved as nothing new of generic value has been learned. *Neocalamites* is still imperfectly separated by morphological characters from *Calamites*; and another Mesozoic genus *Annulariopsis* Zeiller (1903) may well prove to be closely similar. It is a useful group even if not a perfectly defined genus and now includes about six species. Some of these are locally abundant at about the end of the Triassic period, but the genus became rarer in the Lias and the two species described here are among its last known members and even they form a rare element of the flora.

The two species described are distinguished as follows:

Main stems usually 2 cm. wide, internode bundles weakly developed, twice as numerous as leaves. Leaves about 6 cm. long, margins recurved *Neocalamites nathorsti*

Main stems usually 3–5 cm. wide, internode bundles well developed, 2–5 times as numerous as leaves. Leaves about 12 cm. long, margins flat *Neocalamites hoerensis*

Neocalamites nathorsti Erdtman

Text-fig. 7

- ?1894 *Schizoneura hoerensis* Schimper: Raciborski, p. 237, pl. 26, fig. 9; pl. 28, figs. 28–31, 37–43. (Middle Jurassic; Poland.)
 1921 *Neocalamites nathorsti* Erdtman, p. 4, pl. 1, figs. 9–14. (Main stems and leafy shoots. Yorkshire.)
 ?1937 *Neocalamites* cf. *nathorsti* Erdtman: Brick, p. 54, pl. 15, fig. 3. (Similar shoot but with material of other species. Central Asia.)
 1947 *Neocalamites nathorsti* Erdtman: Harris, p. 649, text-figs. 1, 2. (Stems, leafy shoots and leaf details. Yorkshire.)
 ?1957 *Neocalamites* sp., Stanislavski, p. 21, pl. 1, figs. 6–10. (Slender leafy stems. S. Russia.)

EMENDED DIAGNOSIS. Aerial stems sparingly branched or unbranched. Internode length typically 6–8 cm., width 1.3–2.2 cm. Nodes very slightly enlarged. Surface of internode, particularly in smaller stems, marked with longitudinal ridges separating the decurrent bases of adjacent leaves. Interior of stem hollow; when filled with sediment showing vascular bundles; vascular bundles often scarcely discernible in small stems but somewhat stronger in the larger stems, especially near the nodes and frequently obscuring the impression of the

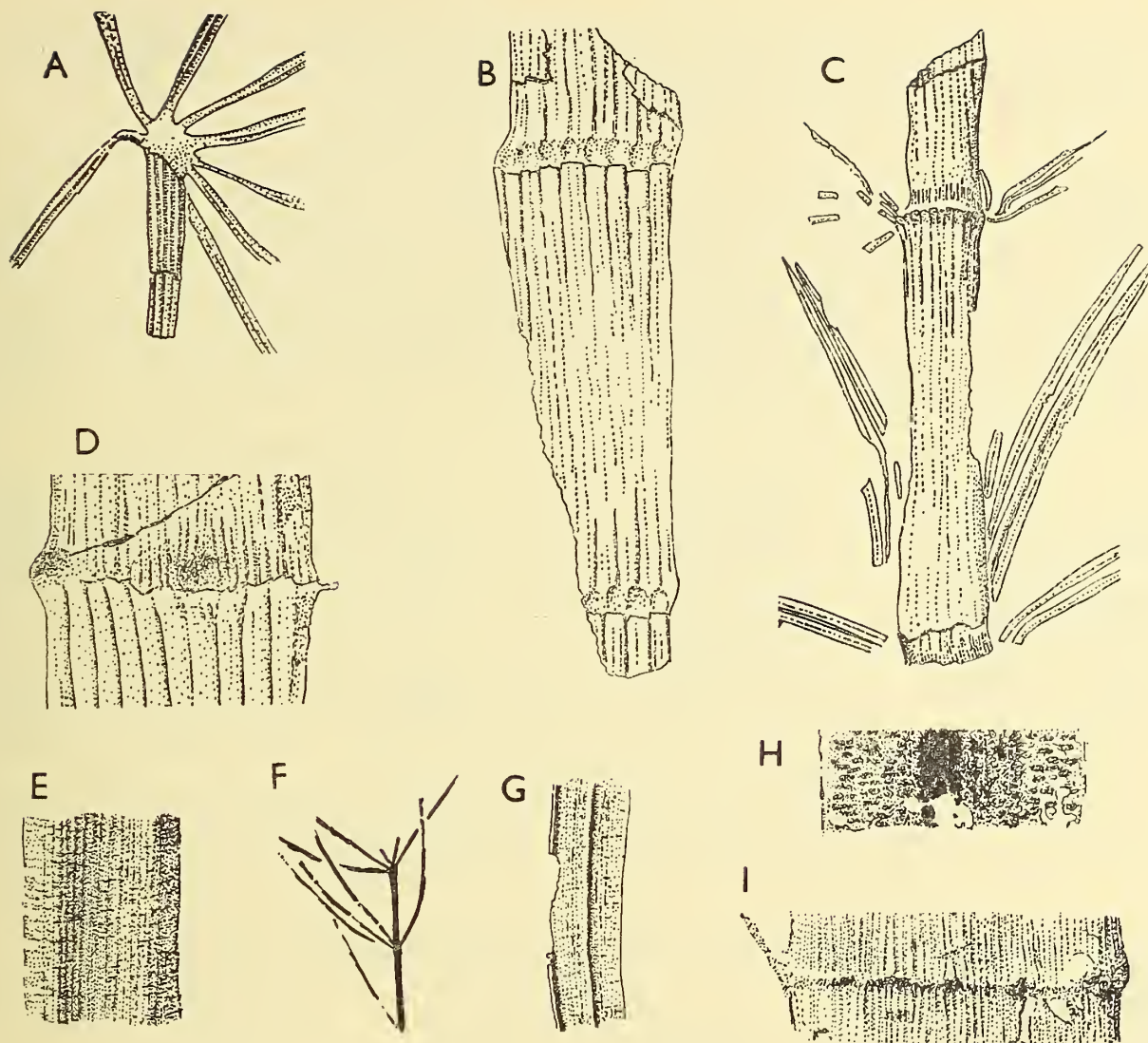


Fig. 7. *Neocalamites nathorsti* Erdtman

A, slender stem bearing a leaf whorl. One leaf is broken off at 6 cm. from the stem, V.27122, $\times 2$. B, impression of medium sized stem with two nodes. The leaves are missing and there are small round marks resembling leaf scars, situated just above the broken decurrent leaf bases, V.27123, $\times 2$. C, medium sized stem with two nodes. The decurrent leaf bases are fairly distinct in the internode and very clear just below the node, but just above the node the vascular bundles become prominent, V.27124, $\times 1$. D, impression of node of medium sized specimen, showing decurrent leaf bases below the node and vascular bundles just above. Two large depressions may represent branch bases, V.27125, $\times 2$. E, upper side of leaf. The midrib is unusually broad; transfer preparation, V.27128, $\times 10$. F, exceptionally small leafy shoot, V.31038, $\times 1$. G, under side of rather narrow leaf showing the keeled midrib and reflexed margins, V.27131, $\times 10$. H, leaf transfer viewed by transmitted light showing transversely elongated cells in the margins, V.27129, $\times 30$. I, node of rather large specimen (? bearing a leaf). The vascular bundles are fairly distinct, V.27130, $\times 2$. All the specimens are from the Whitby Plant Bed, A-E, G, I are reproduced from Harris (1946).

leaf bases. Vascular bundles about twice as numerous as the leaves, 0.5 mm. apart in the larger stems. Cuticle of internode very thin, showing elongated cells, 15 μ wide, with thicker interiors; no stomata observed. Nodal diaphragm unknown.

Leaves normally remaining attached, but occasionally falling and leaving a round scar 1 mm. wide. Leaves of a whorl equal, normally free to their bases, diverging from the base, typically about 6 cm. long. Width 1.0–2.0 mm., typically 1.5 mm., base tapering slightly, apex acute. Margins slightly bent down, entire and parallel in middle region. Midrib rather broad, sunken above, projecting and almost keeled below, marked with longitudinal ridges and containing longitudinal thick strands. Lamina containing transversely elongated dark cells (? transfusion cells) which are more conspicuous in the marginal region than near the midrib. Occasional (detached) leaves preserved in groups of two or more, adhering by their margins from base to apex. Cuticle of leaf unknown.

HOLOTYPE. Specimen figured Erdtman (1921, pl. 1) in Riksmuseum, Stockholm.

DISTRIBUTION. *Neocalamites nathorsti* is frequent in the classic Whitby locality and as there are specimens in old collections it is surprising that it was not described earlier. Main stems have also been identified from Scugdale (V.28532) and main stems and leafy twigs occur together in Beast Cliff (V.31463). These three localities are all Lower Deltaic.

DISCUSSION. *N. nathorsti* is compared below with *N. hoerensis*. It differs from all other species in that its main stems are never large, and the woody strands of the internode are feebly developed. It is most like the Triassic *N. meriani* in appearance, but its leaves are shorter and narrower. A specimen figured by Raciborski (1894) from the Upper Lias of Poland as *Schizoneura hoerensis* Schimper is more like *N. nathorsti*.

In addition to those registered as V.27122–V.27138 other specimens of *N. nathorsti* are to be found in the Riksmuseum, Stockholm; the Yorkshire Museum, York; the Geological Survey Museum (R.C.2458) and in the collection of Dr. H. Hamshaw Thomas at Cambridge.

Neocalamites hoerensis (Schimper) Halle

Text-fig. 8

None of the following is from Yorkshire.

- 1869 *Schizoneura hoerensis* Schimper, p. 283. (Diagnosis, no figure.)
- 1878a *Schizoneura hoerensis* Schimper: Nathorst, p. 24; pl. 10, figs. 6–8. (Good stems. Sweden.)
- 1878b *Schizoneura hoerensis* Schimper: Nathorst, p. 9, pl. 1, figs. 1–4 only. (Good leafy stems. Sweden.) Not p. 40, pl. 1, fig. 5.
- 1908 *Neocalamites hoerensis* (Schimper) Halle, p. 6, pls. 1, 2. (Good main and leafy stems. Sweden.)
- 1922 *Neocalamites hoerensis* (Schimper): Jongmans, pp. 638, 684. (Complete literature up to 1922.)
- 1922 *Neocalamites hoerensis* (Schimper): Johansson, p. 7, pl. 6, figs. 1, 2. (Leafy stems. Sweden.)
- 1926 *Neocalamites hoerensis* (Schimper): Harris, pp. 51, 52, pl. 4, fig. 8; pl. 9, figs. 2, 5; text-fig. 1A. (Leafy stems. Greenland.)
- 1931 *Neocalamites hoerensis* (Schimper): Harris, p. 22; text-fig. 4 A, B. (Leafy shoot. Rhaetic; Greenland.)
- ?1932 *Neocalamites hoerensis* (Schimper): Frentzen, p. 78. No figure. (Stated to occur in Rhaetic of Swabia.)
- 1933 *Neocalamites hoerensis* (Schimper): Kryshstofovich, pl. 5, fig. 3. (Leafy shoot. Bokhara, Turkestan.)

The following are considered to be specifically distinct:

- 1840 *Calamites hoerensis* Hisinger, p. 5, pl. 38, fig. 8. (Discussed by Halle, 1908: 7, 22.)
- 1894 *Schizoneura hoerensis* (Hisinger): Raciborski, p. 95, pl. 26, fig. 9; pl. 27, figs. 28–31, 37–43. (More like *N. nathorsti*.)
- 1915 *Neocalamites hoerensis* (Schimper): Walkom, p. 33, pl. 2, fig. 1. (Stem with more delicate ribs. Australia.)

- 1924 *Neocalamites hoerensis* (Schimper): Walkom, p. 79, pl. 15, fig. 1. (Stem as Walkom, 1915.)
 1926 *Neocalamites hoerensis* (Schimper): Chapman & Cookson, p. 165, pl. 19, figs. 3-5. (Stems as Walkom, 1915.)
 1927 *Neocalamites hoerensis* (Schimper): Du Toit, p. 306. (No figure. Recorded occurrence in Argentina.)
 1931 *Neocalamites hoerensis* (Schimper): Sze, p. 51, pl. 9, fig. 4. (Re-determined as *N. carrerei* by Sze, 1933b: 24.)
 1941 *Neocalamites hoerensis* (Schimper): Brick, p. 7, pls. 1, 2.

EMENDED DIAGNOSIS (based on Swedish and Greenland material). Main stem large, bearing occasional branches. Internode typically 12 cm. \times 4 cm. (sometimes larger); smaller stems with more slender internodes. Nodes without diaphragm, very slightly enlarged. Outer surface of internode nearly smooth in smaller stems but showing ridges due to vascular strands in large stems. Main stems showing conspicuous longitudinal ridges (woody strands) at a concentration of 10-15 per cm.; small stems with less conspicuous and more crowded ridges. In main stem, ridges about 3-4 times as numerous as the leaves, in smaller stems about twice

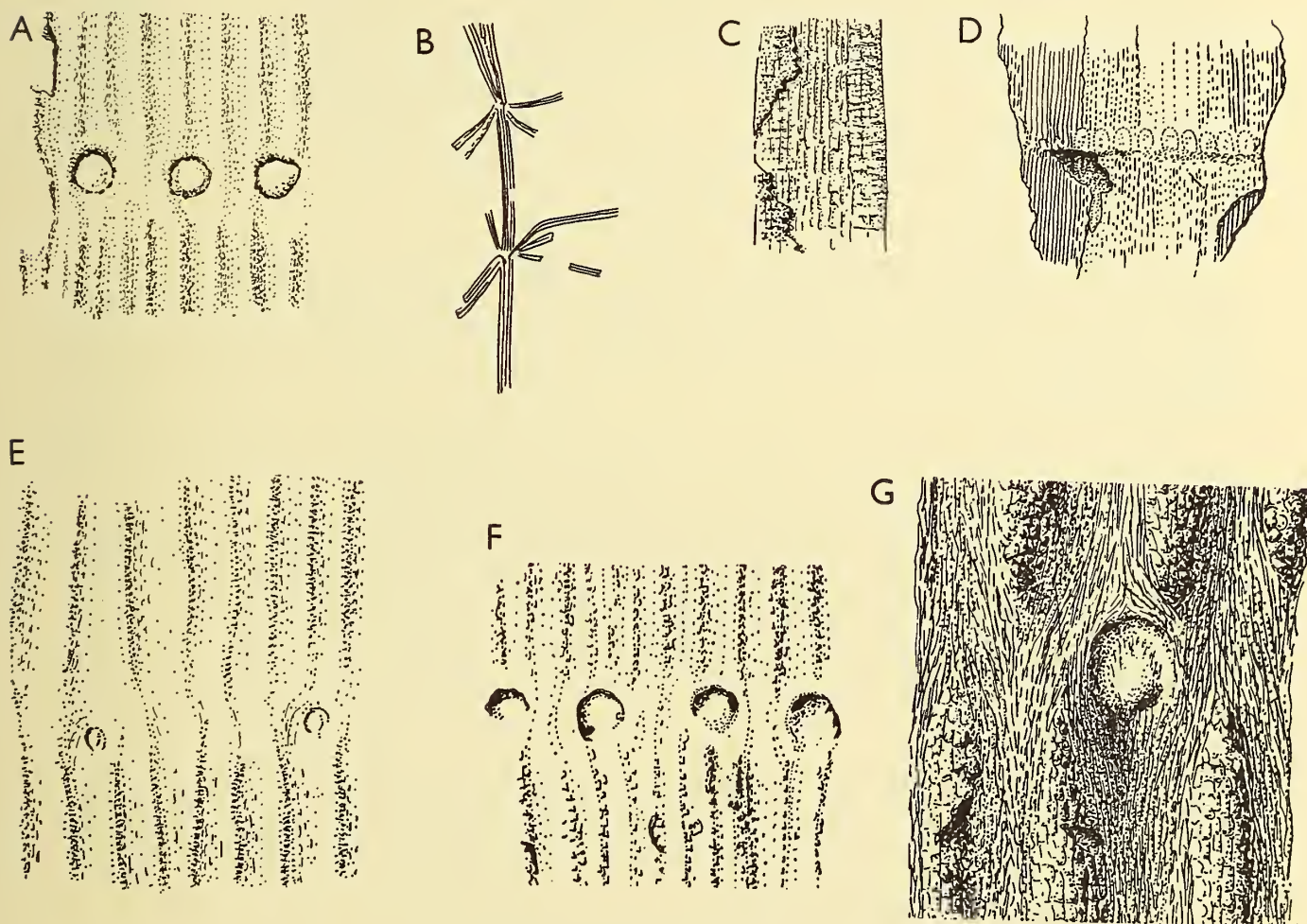


Fig. 8. *Neocalamites hoerensis* (Schimper)

A, details of node, V.31020, \times 8. B, small shoot, V.31026, \times 1. C, leaf, the substance remains on the left only, V.31025, \times 8. D, node showing large scars perhaps of fallen branches. The inner surface with vascular strands is exposed on the left, V.31024, \times 1. E, F, details of node, V.31021-22, \times 8. G, details of node at higher magnification showing the imprints of cells, V.31023, \times 25.

All the specimens are from Cloughton except B which is from Haiburn Wyke.

as numerous, in smallest stems numbers equal. Main stems losing their leaves, medium and small stems usually retaining their leaves.

Leaves of a whorl equal, typically about 12 cm. long, about 2 mm. wide in the middle and basal thirds, but tapering in the upper third. Midrib broad, rather ill-defined, not keeled; margins entire, flat; lamina showing rather large transfusion cells.

Cuticle of stem and leaf unknown.

DISTRIBUTION. *N. hoerensis* occurs in a small part of the Middle Deltaic 'quinqueloba Bed' at Cloughton Wyke in vast numbers of fragments, and this may be what Nathorst noticed and mentioned in 1880. In addition, there are a few fragments of typical main stems from the Lower Deltaic, from Ryston Nab Quarry and from Roseberry Topping (collected by Miss Kendall) and an exceptional main stem collected by Dr. Hamshaw Thomas from Haiburn Wyke, and there are some small twigs in a layer just above the plant bed.

DISCUSSION. The twigs from Haiburn Wyke could just as well belong to *N. nathorsti*, but Dr. Thomas' main stem could not, but it matches a few of the Cloughton specimens. It shows a whorl of scars of small branches at the node. It should be pointed out that no main stems bearing whorls of scars of small shoots in this way have been figured in Rhaetic material of *N. hoerensis*. There is unlikely to be any real distinction in this respect, however, between the Oolitic and the Rhaetic material because the fairly frequent occurrence of slender stems known in the Rhaetic were most probably borne in just this manner.

Most of the Cloughton specimens are fragments of large stems. Internodes 3 cm. wide are common, but fragments over 4.5 cm. wide were noted, and also internodes over 12 cm. long. The coaly ridges (vascular bundles) of the internode are usually clearly marked; they occur at a concentration of 10-15 per cm. and in different stems the ratio of bundles to leaf scars varies between 2 and 5.

Although the specimens are too much broken to add to knowledge of the gross form they show their fine details well; and transfers gave some new information.

The surface exposed is usually the outer one on which the leaf bases form little cups, the leaf scars are not seen at all on the inner surface of the node. Usually the edges of the leaf base cup are broken off; when complete the cups are very prominent. The fine details of the outer surface of the internode agree with Halle's account, the broad parenchymatous cells being very clearly marked off from the narrow ones of the vascular ridges. At the node the narrow cells can be seen running obliquely to join the new bundles or else passing into a leaf base. The inner surface shows no trace of a nodal diaphragm. The internodal bundles are rather more prominent than on the outer surface (and hence less often exposed), but their cellular markings and those of the intervening ray are almost the same as on the outside. No specimen shows decurrent leaf bases such as are seen in *N. nathorsti*, but I cannot say whether the outer surface of the fossil is the true outer surface of the stem or only that of the vascular core. Better material would repay study.

No intact leafy stem was found at Cloughton, but a number of isolated leaves occur with the stems. They vary from 1.2-2.2 mm. wide. They show a broad midrib with vertically elongated cells and a lamina with transversely elongated cells. The substance is thick but fragile, the midrib is not specially prominent on either side, and the margins are quite flat.

Had the Yorkshire material been Rhaetic I would have identified it as *N. hoerensis* without hesitation as the agreement is very good. Because its age is very different, it has been identified

with reluctance, particularly because *N. hoerensis* seemed a valuable Rhaetic zone fossil, disappearing before the Lower Lias. If this Yorkshire material is ever to be separated from that of the Rhaetic, more will have to be learnt about it and about the Rhaetic material as well.

Genus SCHIZONEURA Schimper & Mougeot, 1844:50

Schizoneura is common in the Permo-Carboniferous of Gondwanaland and the type species, *Schizoneura paradoxa*, is widespread in the European Triassic, but there are very few younger species. Apart from those removed to the genus *Neocalamites* by Halle (1908) and to *Lobatanmularia* by Kawasaki (1932) there are two incompletely known Jurassic species, *S. algarbensis* Teixeira and *S. ferganensis* Kryshstofovich, both based on separate fragments of different organs which do not prove conclusively that the leaves are borne in the *Schizoneura* manner. The present specimens, however, have their leaves intact and are very like *S. paradoxa*.

Two different looking cones have been referred to *Schizoneura*, *Aethiophyllum speciosum* Schimper & Mougeot (see Magdefrau, 1936) and *S. gondwanensis* (see Arber, 1905: 9). No cone occurs with the Yorkshire specimens.

Schizoneura stenophylla sp. nov.

Text-fig. 9

DIAGNOSIS. Stems 5–7 mm. wide, internodes 3–5 cm. long, nodes very slightly expanded, no diaphragm present. Internode with about 16 longitudinal woody strands forming conspicuous ridges on the pith cast and less conspicuous ridges on the outer surface; each strand giving off one leaf bundle at the node and alternating with strands in next internode. Outer surface of internode showing longitudinal cellular ridges 60 μ wide and probably subordinate finer ridges; also showing large and irregular transverse wrinkles. Stomata not apparent. Pith cast showing obscure marks of small cells.

Leaves often forming three or four groups usually of four leaves, but occasionally of eight, in each group. Whole group typically 10 cm. long, twisted and slightly narrowed at the base but of nearly uniform width over most of the length, then gradually tapering to an acute point and normally remaining united to the point. Individual leaves reaching a width of 1.5–2 mm. Midrib and margins both depressed, midrib often showing two or more subordinate longitudinal ridges, lamina showing fine longitudinal cellular striations and coarser transverse cellular striations.

HOLOTYPE. V.35320.

OCCURRENCE AND DISCUSSION. The present specimens were found in 1957 in a block of clay-ironstone fallen from the Lower Deltaic Beast Cliff, near Prospect House. The matrix contained several very similar specimens and little else. There is a little matrix inside the stems (but not enough to give good pith casts). The longitudinal ribs on the stem are often obscure, usually the surface shows about eight ridges caused by the main woody strands, but parts of the holotype seem to show four ridges, each faintly scored by a furrow, while other parts show numerous fainter ridges.

The leaf-groups show their individual leaves when viewed directly, and particularly when immersed in oil when their dark midrib and separate margins are clear. The rock impression, however, often seems to show twice as many leaves as there really are as the imprint of the

midrib looks just like the imprint of the margins. The leaves remain in groups rather persistently; the only ones which are separate look to have been mechanically damaged before preservation.

The ironstone matrix preserves the original contour of fossils very well (the famous solid *Williamsonia gigas* flowers occur in such a rock), but cuticles suffer and it is impossible to say whether one was present. It does not, however, cleave well, and this is why so many of the leaf groups in the holotype appear isolated. Some damage has also been caused by the sediment slumping.

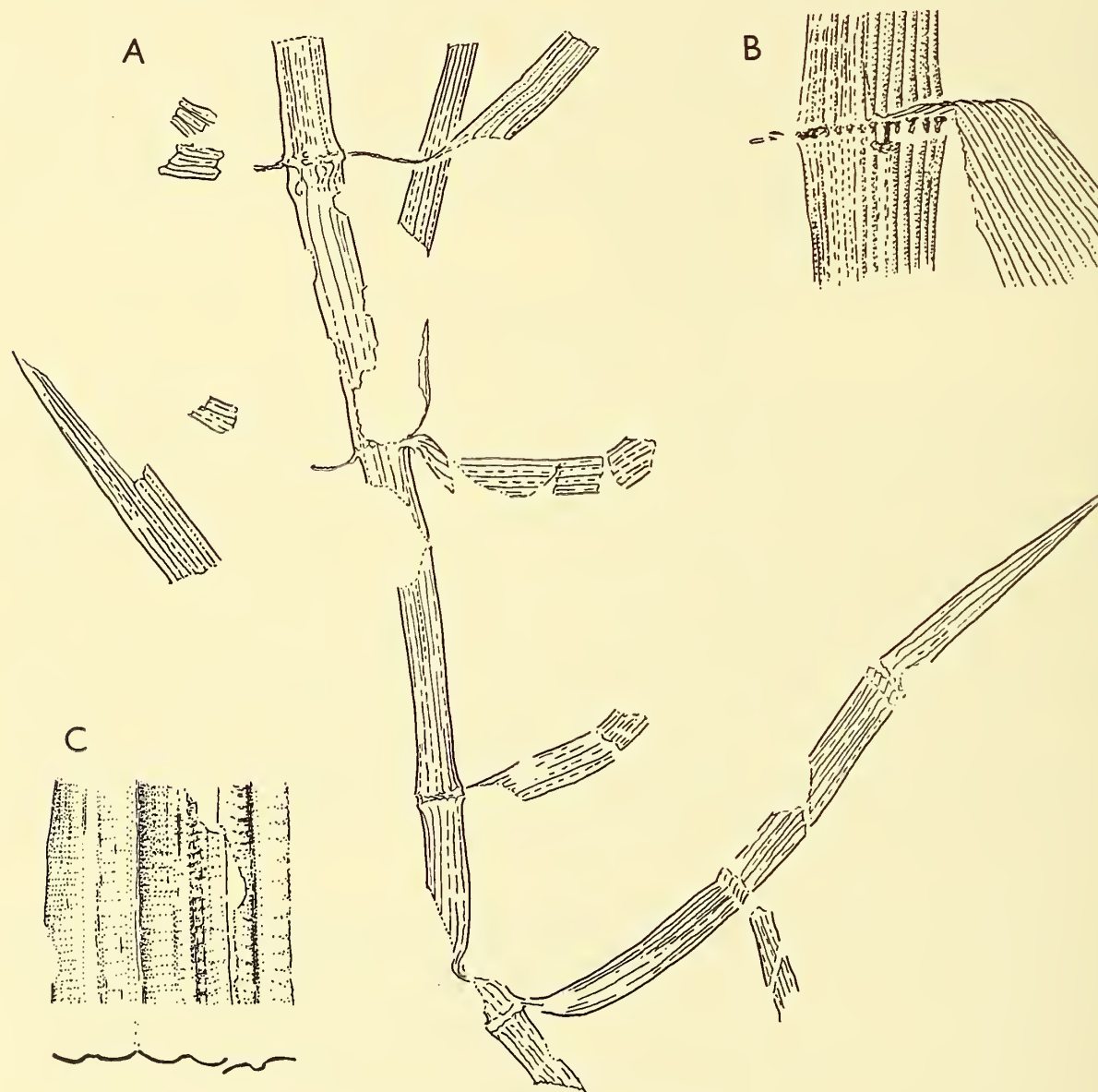


Fig. 9. *Schizoneura stenophylla* sp. nov.

A, Holotype, V.35320, natural size. A few leaf portions outside the figure are omitted. B, node bearing a leaf with eight segments, V.35321, $\times 2$. C, damaged leaf group, two leaves still joined are seen from below and one displaced is seen from above. The diagram below indicates the surface contour, V.35322, $\times 6$. All from Beast Cliff.

COMPARISON. *Schizoneura stenophylla* is close to *S. paradoxa* but has narrower leaves (1.5–2 mm. instead of about 3 mm.), they are also longer and their apices are more gradually attenuated. No larger stems like those of *S. paradoxa* are known in *S. stenophylla*.

S. gondwanensis, the most similar of the Gondwanaland species has shorter and broader leaf-groups made up of more segments.

Both the Jurassic species have much broader leaf groups. In *S. algarbensis* Teixeira from Portugal they are finely striated and look like *Sphenozamites* leaves, as Teixeira (1948) remarks. In *S. ferganensis* Kryshstofovich (1933) from Siberia, the leaf group has some 20 segments diverging from a point. Brick (1937: 58) referred some stems to the same species.

The only Yorkshire fossils at all resembling *S. stenophylla* are the species of *Neocalamites*, particularly *N. nathorsti*, but their leaves, though similar in details, are always free. The vascular bundles behave differently at the nodes.

Genus ANNULARIOPSIS Zeiller, 1903:132

This genus is used for whorls of small lanceolate one-nerved leaves borne in a terminal position probably through the breaking off of the stem or bud above. Nothing is known but these twigs and only two Mesozoic species have been recognised. It is distinguished from *Phyllothea*, *Schizoneura* and *Lobatannularia* by the leaves being free to their bases and differs from the leafy twigs of *Neocalamites* chiefly in that the *Neocalamites* shoots do not ordinarily break just above a leaf whorl but bear successive whorls. (Most probably the end of the shoot was shed early in *Annulariopsis* since the scar is very small.) The same difference distinguishes it from most of the Carboniferous species of *Annularia* and of *Asterophyllites* but often isolated *Annularia* whorls occur looking very like *Annulariopsis*.

A genus of such imperfect circumscription can hardly be satisfactory and different authors have merged it with *Lobatannularia* or else with *Neocalamites*, but I agree with Kawasaki (1931: 65 *et seq.*) that it is best kept separate.

Annulariopsis simpsoni (Phillips) n. comb.

Text-fig. 10 A–E

1. Yorkshire specimens.

- 1828 'Head resembling Honey-suckle', Young & Bird, p. 191, pl. 1, fig. 3. (Drawing of leaf whorl.)
- 1875 *Marzaria simpsoni* Phillips, p. 204, lign. 13, 14. (Drawings of leaf whorl.)
- 1900 '?*Laccopteris polypodioides*' (Brongn.): Seward, p. 82, text-fig. 9 only. (Specimen of Young & Bird and of Phillips refigured.)
- 1910 '?*Laccopteris polypodioides*' (Brongn.): Seward, p. 360, text-fig. 268. (As Seward, 1900.)
- 1947 *Annulariopsis simpsoni* (Phillips) Harris, p. 654, text-figs. 3, 4 A–D. (Details of leaf, discussion of morphology.)

2. Possible specimens from other regions.

- ?1932 *Annulariopsis inopinata* Zeiller: Oishi, p. 271, pl. 21, fig. 5 only. (Fragment. Japan.)
- ?1933 *Annulariopsis inopinata* Zeiller: Kryshstofovich, p. 126, pl. 5, fig. 1. (Leaf whorl. Ferghana, Central Asia.)
- 1936 *Annulariopsis inopinata* Zeiller: Oishi & Takahasi, p. 116, text-fig. 2. (Leaf whorl. Japan.)
- ?1940 'Matonia-like fronds' Sitholey, p. 7, pl. 2, figs. 20–30; pl. 7, figs. 93–97 (not text-figs. 2, 3). (Good leaf whorls. Afghanistan.)
- ?1940 *Phlebopteris pentaphylla* Oishi, p. 204, text-figs. 5, 5a, 6, 7. (Leaf whorls. Japan.)
- ?1957 *Annulariopsis inopinata* Zeiller: Stanislavski, p. 20, pl. 1, figs. 2–5. (Leaf whorls. S. Russia.)

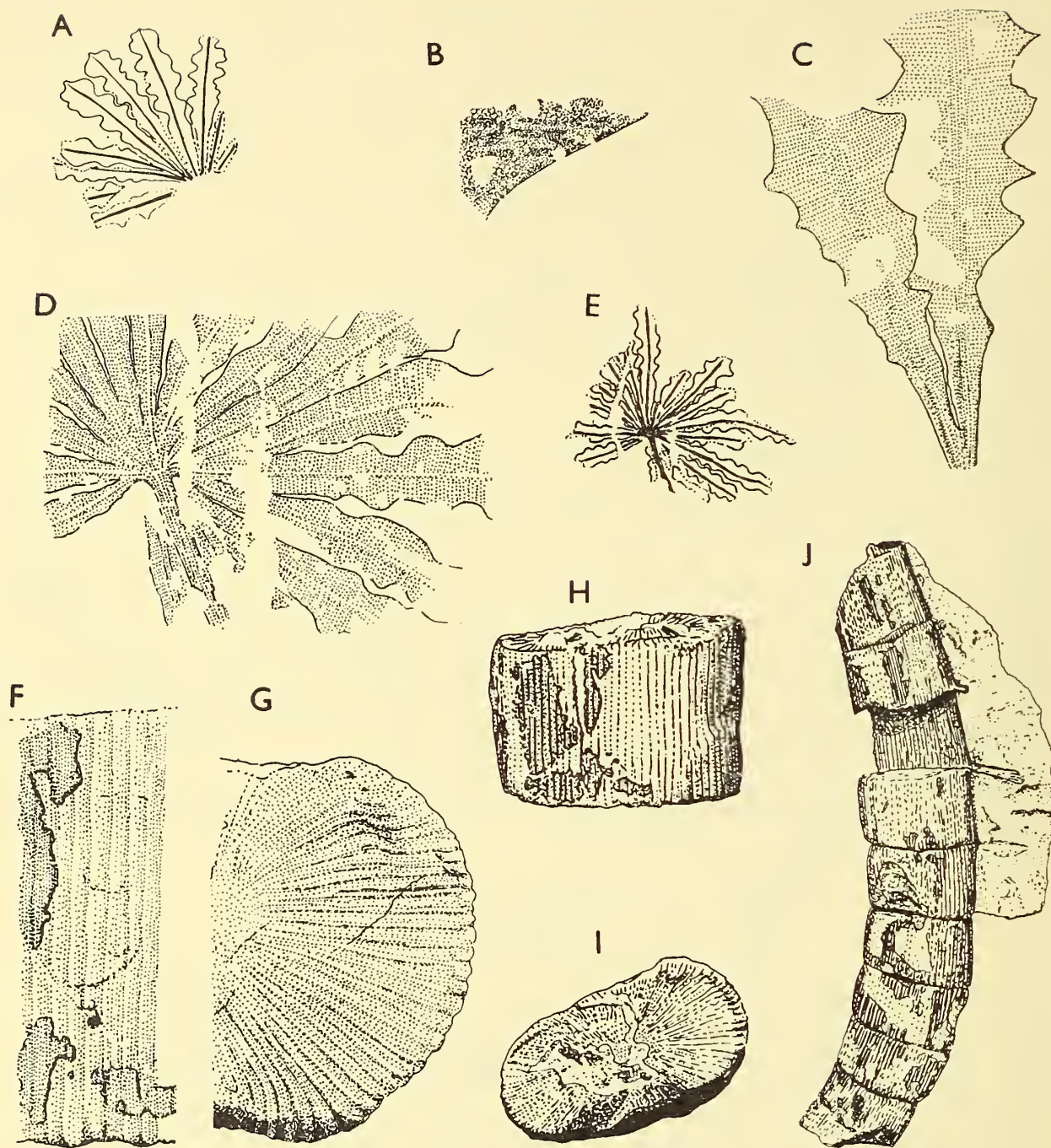


Fig. 10. *Annulariopsis simpsoni* (Phillips), *Calamites* (?) *rotifer* sp. nov.

A-E, *A. simpsoni*. A, part of leaf whorl showing apices, V.31051, $\times 1$. B, part of C showing the elongated dark cells and the margin, $\times 30$. C, transfer preparation of two leaves, V.27142, $\times 4$. D, part of specimen shown in E, $\times 4$. E, leaf whorl and stem, V.27139, $\times 1$. All the specimens are from Whitby Plant Bed. B-E are from Harris (1947). F-J, *Calamites* (?) *rotifer*. F, part of surface of internode showing ridges, $\times 1$. G, part of diaphragm showing spokes, $\times 1$. H, I, two views of isolated internode reduced to one-third natural size. J, whole specimen at one-sixth natural size (ridges partly diagrammatic). The segment seen in H, I, is from below the base of J. (V.1024).

DIAGNOSIS. Ultimate branches slender, about 1 mm. thick, surface marked with longitudinal ridges (possibly equalling the leaves in number). Leaves borne in a terminal whorl, persistent, equal in size, radiating almost horizontally. Adjacent leaves united for about 1 mm. at the base, then free. Leaf linear, about 3 cm. long, middle region 3–6 mm. wide, tapering at the base. Margins of leaf entire below, then becoming strongly sinuous or forming obtuse teeth. Leaf flat, midrib not prominent (except at the base where the margins also are slightly reflexed), midrib becoming narrower but denser in substance towards the base. Lamina delicate, showing at least two sets of cells, namely small polygons (? epidermis) and also transversely elongated dark cells (? transfusion cells) which sometimes form perceptible surface striations. Margin flat, slightly reinforced by a single layer of dark cells. Cuticle of stem and leaf unknown, probably very delicate.

HOLOTYPE. Specimen no. 2379, Whitby Museum.

DISTRIBUTION. *A. simpsoni* occurs rather rarely in the Whitby plant bed and is recorded at 'Hawsker Bottoms' which is taken to be the Lower Deltaic cliffs by the Jack Ass Trod. I have collected one specimen from the Beast Cliff *Otozamites* Bed.

DISCUSSION. Unfortunately this fossil became known under the generic name of *Marzaria* Zigno, a synonym of *Phlebopteris* (or *Laccopteris*) and so, being wrongly placed was missed from the Equisetales.

All the specimens seen show the leaves in a terminal position on the shoot and I am convinced that the continuation of the stem was lost before preservation. One specimen suggested a small terminal scar, similar to that figured by Zeiller (1903).

A. simpsoni differs in its dentate leaf margins from the Rhaetic species *A. inopinata* and from the leaves of all species of *Neocalamites*. The leaves seem to be similar to those of *Neocalamites* in their midrib and transfusion tissue but are more delicate than either *N. nathorsti* or *N. hoerensis*.

There are good specimens of *A. simpsoni* from Whitby in the Riksmuseum, Stockholm.

Genus CALAMITES Schlotheim, 1820:398

The stem described here looks very like the familiar *Calamites suckowi* in its internode though the nodal structure distinguishes it. It proves the existence of a plant with large, rather woody, main stems more like the Palaeozoic *Calamites* than anything yet recognised in the Mesozoic, and it is considered better placed in *Calamites*, using that designation in its broad sense, than in *Neocalamites* which has definite characters of leaf arrangement that are not known here. None of the Palaeozoic species known to me has a diaphragm like *C. rotifer* but a slight approach is perhaps seen in the specimen figured by Lindley & Hutton (1832, pl. 20) called 'phragma of a *Calamite*'. It differs from *Equisetum* in the large and presumably woody internodal strands.

Calamites(?) *rotifer* sp. nov.

Text-fig. 10 F–J

DIAGNOSIS. Main axis up to about 10 cm. wide, showing slightly constricted nodes at intervals of 5–15 cm. Surface of internode marked by about 120 shallow longitudinal grooves. Grooves (probably woody strands) 1 mm. wide, separated by ridges 2 mm. wide. In smaller

stems grooves narrower and at intervals of 1.5 mm. No cuticle present. No nodal prints present, strands of successive internodes alternating. Nodal diaphragm robust, composed of radiating spokes, slender near the centre but becoming stouter (nearly 1 mm. wide) towards the outside, each spoke being opposite one vascular strand of the internode. Centre of diaphragm forming a continuous but delicate disc.

Leaf sheath and leaf unknown, but occasional small branches present, nearly 1 cm. thick, showing about 6 internodal bundles.

HOLOTYPE. A sandstone cast (V.1024).

OCCURRENCE. 'High Whitby.' Presumably a fallen block from the Lower Deltaic Cliffs.

DISCUSSION. The holotype is a striking fossil consisting of a sandstone cast nearly 60 cm. long lying in its mould. The stem lay horizontally and the cast measures only half as high as it is broad, but as it shows obvious signs of deformation it is to be assumed that it is crushed and may well have originally been round. The matrix is a hard, fine grained sandstone and the fossil forms a film of coal except at the node where it is partly replaced by kaolin. The specimen has no original label, and was recently transferred from another Department. It bears the name '*E. columnare*' but this is certainly wrong; nor can it be *E. beani* (with which it agrees in size) because both the surface of the internode and the nodal diaphragm are different. The diaphragm indeed resembles that of *E. laterale* in its spokes, but they agree in nothing else. It is certainly distinct from any known Jurassic stem.

There is probably a second specimen of this species in the Natural History Museum, Wollaton Hall, Nottingham. This is a large piece of grey shale bearing many fragments of compressed stems (not solid casts like the holotype). The largest fragment has an internode exceeding 15 cm. in length. The internode and node look just the same as in the holotype except that the nodal diaphragm is not seen. The specimen is merely labelled, 'Inferior Oolite, Yorkshire Coast'.

The possibility was seriously considered that this species is a Carboniferous *Calamite*, the specimens having been displaced in a collection and afterwards labelled with a false locality. I have in fact met a few Carboniferous plants in several large Jurassic collections. I rejected this for the following reasons:

(1) No Carboniferous *Calamite* has a diaphragm just like *C. rotifer*. Very few species have diaphragms at all.

(2) The Nottingham Museum specimen has the label 'Inferior Oolite, Yorkshire Coast'. It seems to have been of quite independent origin since it is preserved in a different matrix and should therefore be from another locality and most probably by a different collector. It is included in a collection of typical Yorkshire Deltaic fossils with similar labels. Although the history of the holotype is less well documented than is usual with British Museum specimens, and no relevant details are known about the Nottingham specimen either; the idea seems too improbable to entertain that the only two known specimens of a Carboniferous fossil should both have been misplaced and then falsely labelled.

The late W. J. Jongmanns pointed out the existence of a large nodal diaphragm which is perhaps comparable with this, namely the 'Diaphragm of Type 1' of *Equisetites arenaceus* described by Frentzen (1933: 32, pl. 1, fig. 1). This differs from that of *C. rotifer* in being very convex instead of flat. As, however, a second and quite different type of diaphragm is also attributed to *E. arenaceus*, it is clear that further investigation is needed.

LYCOPODIALES

Genus LYCOPODITES Lindley & Hutton, 1833:170

TYPE SPECIES. *Lycopodites falcatus* L. & H.

Lycopodites taxiformis Brongniart (1822) is a conifer according to Seward (1910: 76) and *Lycopodites* of Lindley & Hutton is a homonym but the required change of name is left until the fossil is better understood. *Lycopodites* has been used for various plants, including Conifers, Lepidodendraceous twigs and even an Hepatic (*Naiadita*). There is no case for including this species in *Selaginellites* Zeiller (1906).

Lycopodites falcatus was originally compared with *Lycopodium complanatum* (*Selaginella* not being mentioned), but later authors inclined to regard it as a *Selaginella*. The present study confirms that it is a Lycopod and while not conclusive, supports the affinity with *Lycopodium* and it may well be a species of the living genus. Other possibilities were that *L. falcatus* might be a large dorsiventral Bryophyte, but this is ruled out by the stomata in the leaf, or that it might be a Conifer, but this is ruled out by the lack of any cuticle. The two genera *Lycopodium* and *Selaginella* differ in three main characters—stele (here unknown), ligule (hardly to be observed in such material) and heterospory (only determinable with good nearly mature cones, not here available). They differ also in a number of other characters, none of which is constant and which must therefore be regarded as subsidiary, but all of those here available point to *Lycopodium* rather than *Selaginella*. These are firstly the phyllotaxis; in *Selaginella* species with dorsiventral shoots the phyllotaxis is usually decussate, with two ranks of small upper leaves and two larger under leaves, or occasionally it approaches this but is rather irregular. In *Lycopodium* it is much more varied and sometimes complex; for instance in *L. complanatum* there are large lateral leaves and small ventral and dorsal ones, the number of small ventral leaves being half that of the dorsal or lateral. The arrangement in *L. falcatus* is by no means clear, but—there are probably two dorsal and two ventral ranks with equal numbers and each dorsal rank is only half as numerous as the lateral leaves. This is not exactly as in *L. volubile* or *L. complanatum* but much nearer that than *Selaginella*. Secondly, there is no leaf at all in the angle of a dichotomy. Such a leaf is characteristic of *Selaginella* but absent in *Lycopodium* and this is confirmed by many excellently preserved dichotomies of *L. falcatus*. Thirdly, the shape of the lateral leaves which are laterally compressed and longitudinally attached, is exactly as in *L. volubile* and some other complanate *Lycopodium* species and entirely foreign to *Selaginella*. The distribution of stomata is again in agreement with *Lycopodium* while in *Selaginella* they are confined to the midrib of the lower side. I do not think that the leaves of *L. falcatus* were originally exceptionally delicate, but rather comparable with most fern leaves; in beds like the 'quineloba Bed' where no oxidation seems to have occurred they are black, opaque and moderately thick. It is where other fossils are slightly oxidised and fern leaves also are represented by a brown epidermal film enclosing vascular strands that *Lycopodites* occurs in this state.

The associated cones (which have not yet been proved to belong to *L. falcatus*) if accepted would support the *Lycopodium* affinity. The shape of the sporophyll is more like that of *Lycopodium*. The tendency of the sporophyll lamina to fall off is not known to me in either genus.

The form of the sporangia (they are all empty) suggests that they are all alike, and those seen are either homosporous, or else represent the microspore producing part of a *Selaginella*. I searched the matrix in which the shoots are preserved for megaspores and found none but this is not very significant (though had megaspores been found strikingly associated I would have used them as evidence in favour of *Selaginella*). Although no megaspores are closely associated with *L. falcatus*, other parts of the three rich beds in which it occurs yield several species of megaspores.

To summarise, *L. falcatus* is almost certainly a Lycopod. There is no evidence pointing to affinity with *Selaginella* but a good deal of not fully conclusive evidence pointing to *Lycopodium*. It may be noted that this fossil has already been placed in the living genus *Lycopodium* by Schimper (1870) but our knowledge does not justify this step.

Another Jurassic fossil which apparently has affinity with *Lycopodium* is *Lycopodoxylo*, an isolated petrified stem from India.

Lycopodites falcatus L. & H.

Text-figs. 11, 12

The following are all Yorkshire specimens.

- 1828 'Small round crowded sessile leaves' Young & Bird, p. 192, pl. 2, fig. 7.
- 1833 *Lycopodites falcatus* Lindley & Hutton, p. 171, pl. 61. (Good shoot.)
- 1875 *Lycopodites falcatus* L. & H.: Phillips, p. 6, lign. 6. (Sketch of leaves.)
- 1900 *Lycopodites falcatus* L. & H.: Seward, p. 69. (Discussion.)
- 1910 *Lycopodites falcatus* L. & H.: Seward, p. 83, text-fig. 137. (Good leafy shoot.)

EMENDED DIAGNOSIS. Main stems up to 2 mm. thick, nearly straight, sparingly branched. Main lateral branches 1 mm. thick forking rather unequally but exclusively in one plane (the stronger branch alternately right and left), angle of earlier dichotomies about 70° but reduced to 40° near the apex. Leaves of main stems isophyllous, small, borne in pairs or whorls at rather long intervals and pressed against the stem.

Branch stems strongly complanate in their branching and in their foliage. Foliage consisting of spreading lateral leaves and small appressed dorsal and ventral leaves. Lateral leaves usually alternate, but sometimes nearly opposite or irregular, spreading at right angles to the stem. Dorsal and ventral leaves small, similar to one another, probably each forming two ranks but less numerous than lateral leaves.

Lateral leaves well spaced on main branches but crowded and overlapping towards the apices. Shape laterally compressed, attached longitudinally with a slightly contracted upper margin and a distinctly decurrent lower margin. Lamina falcate, at first spreading at right angles to the stem, but apex curving forwards or even slightly inwards. Margins varied, partly entire, partly irregularly denticulate. Vein single, slender, course sigmoid. Dorsal and ventral leaves dorsiventrally flattened and more or less appressed to the stem or with the free apex partly overlapping a lateral leaf. Apices of successive leaves inclining to the right and left and probably forming two ranks. Shape more or less lanceolate, apex irregularly rounded but usually with a delicate apiculus, bases strongly decurrent, margins denticulate, vein single, slender.

Substance of all leaves rather delicate, leaf consisting of the two epidermises, some mesophyll tissue and the vascular bundle but without fibres or hypodermis. Stomata scattered

over the whole of both surfaces (except at the extreme edge). Epidermal cells with rather thick, sinuous lateral walls but no special surface markings; cuticle absent.

Associated cones slender, unbranched for at least 3 cm. Sporophylls probably whorled, consisting of a horizontal pedicel, an upward pointing lamina and a slight downward pointing heel at the angle of pedicel and lamina; sporophylls commonly breaking off at maturity just beyond the sporangium. Sporangia axillary, rounded, about 0.75 mm. wide, wall cells very sinuous.

HOLOTYPE. Specimen figured Lindley & Hutton (1833, pl. 61). Regd. no. 39314.

DISTRIBUTION. *L. falcatus* occurs in the *quinkeloba* Bed at Cloughton Wyke. Dr. Hamshaw Thomas' material is from Gristhorpe, and from the *Solenites* Bed at Cloughton; these

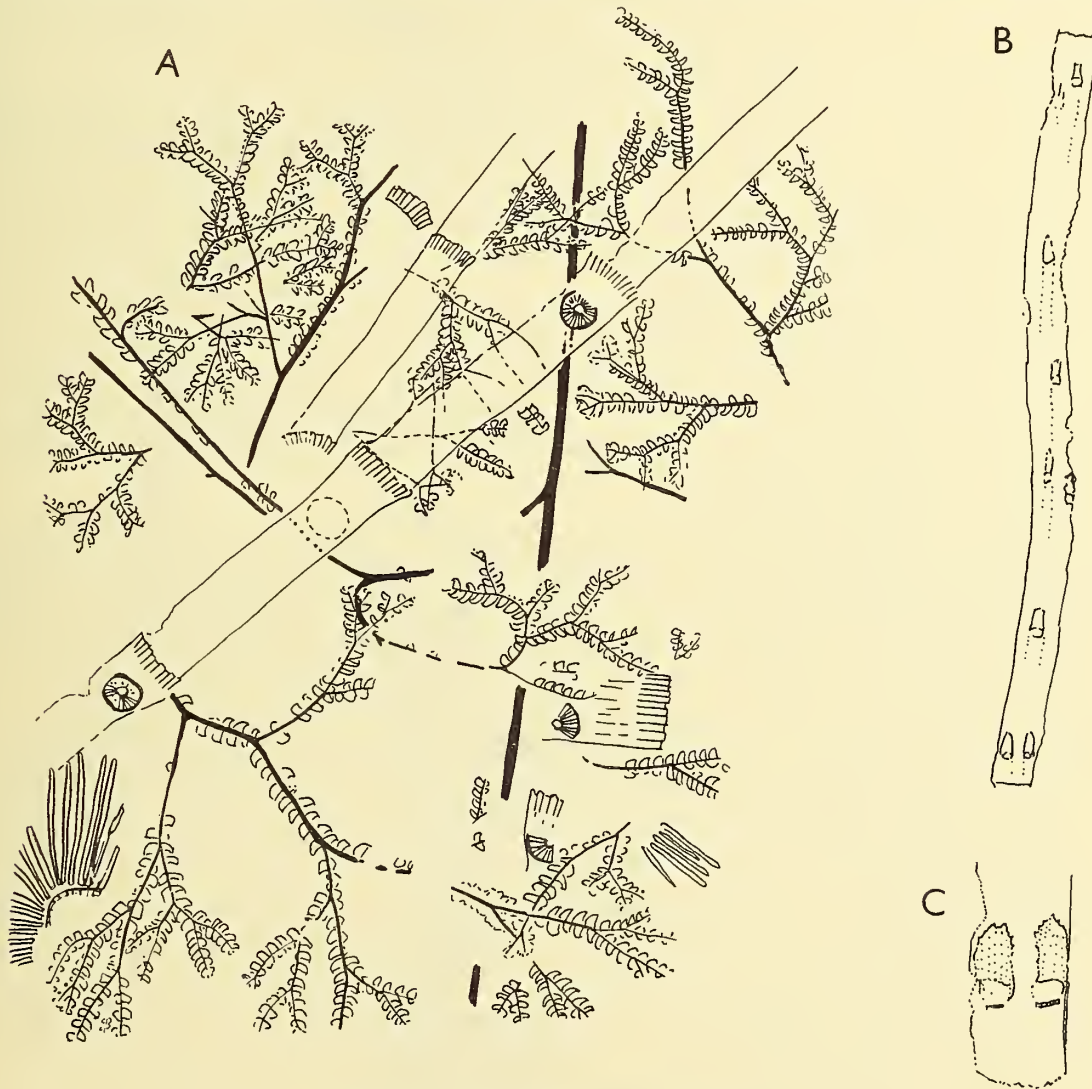


Fig. 11. *Lycopodites falcatus* L. & H.

A, portion of a specimen in the Yorkshire Museum showing a main stem and several shoots; also part of a stem of *Equisetum laterale* 22 cm. long, and isolated fragments. Specimen 60:2.46, unlocalised. B, main stem of *L. falcatus* showing the leaves. Cloughton Wyke *quinkeloba* Bed, V.31052, $\times 4$. C, two lowest leaves of B, $\times 10$.

three beds belong to the Middle Deltaic, Gristhorpe Series. The Yorkshire Museum specimen is not properly localised. Lindley & Hutton record it from 'Cloughton' and 'either Saltwick or Hawsker Cliffs' (Lower Deltaic), but it is not known whether the determination is reliable.

There is a good specimen of *L. falcatus* in the Manchester Museum.

DISCUSSION. The only large specimen seen is a slab of sandy shale in the Yorkshire Museum about half of which is shown in Text-fig. 11. It is probable that many or all of the branches were originally connected but this cannot be proved as the specimen is worn and the counterpart missing. All the other specimens are smaller fragments on soft shales and here the substance often sticks in separate crumbs to part and counterpart making investigation troublesome. The most perfectly preserved fragments are some collected by Dr. Hamshaw Thomas from the Gristhorpe Bed which seem to have been oxidised before preservation and consist of little more than epidermis and vascular tissue.

Previous authors have all seen the small leaves but found difficulty in making them out well enough to figure and though I have obtained some good ones I found it very hard to be sure of the phyllotaxis. I have, however, proved repeatedly that the small leaves occur on both sides of the stem and that those on either side are less numerous than the lateral leaves, and that the lateral leaves are attached longitudinally. It is doubtful whether the lateral leaves form two real ranks for they overlap their neighbours in front and behind irregularly and occasionally there is a small lateral leaf which seems intermediate between an ordinary lateral and a dorsal one. One specimen which showed some of the lateral leaves nearly opposite one another and usually one 'dorsal' leaf for each pair when transferred showed roughly one 'ventral' leaf to each pair, but this was by no means clear, it is uncertain whether the arrangement approximates more closely to whorled or decussate.

In the more transparent (naturally oxidised) leaves the epidermal cells of the two sides are clearly visible, and occasionally those of one side are more plain (as in the leaf figured). In all leaves stomata are generally distributed and since superimposed stomata are seen, they must be present on both sides, though not necessarily in equal numbers. The unoxidised specimens (from the Cloughton *quinqueloba* Bed) are, however, almost entirely opaque.

Four fragments of ill-preserved cones occur associated with the numerous shoots in Dr. Hamshaw Thomas' material from Cloughton. In three of them the sporophylls seem to have broken off leaving some of the sporangia exposed, but one still has some of the sporophylls. These cones are unlike anything I have seen elsewhere and they probably belong to *L. falcatus* though there is no proof. All the sporangia seen are similar in size and are empty.

Celloidin pulls show the sporangial wall cells which are very sinuous and serve to identify the different cones with one another (though they do not provide evidence that they belong to *L. falcatus*). Satisfactory views of the cells of the sporophyll laminae could not be obtained.

Search was made for megaspores in the matrix but none was found, and though doubtless with more material a few would have been found, it can be stated that megaspores are not notably associated with the shoots in any of Dr. Hamshaw Thomas' material, nor in that from the *quinqueloba* bed. The bedding plane of Dr. Hamshaw Thomas' specimens, however, shows numbers of small spores of several types, mostly belonging to ferns. Spores of one kind are particularly numerous round two of the cones and some are figured sticking to the sporangial walls but they are very likely fern spores (Text-fig. 12 E).



Fig. 12. *Lycopodites falcatus* L. & H.

A, B, cone fragment, V.31055, A $\times 16$; B $\times 8$. C, sporangia from the main cone in G, $\times 16$. D, leaf cells (the under epidermis is only faintly seen, Gristhorpe Bed, V.31058, $\times 200$. E, piece of sporangium wall from the cone seen in B; also the commonest associated spores (? fern), $\times 200$. F, sporangium from the smaller cone fragment in G, $\times 16$. G, two cones, showing axis and sporangia only, V.31056, $\times 4$. H, leafy shoot, V.31057, $\times 4$. I, middle part of the shoot seen in H, $\times 16$. All except D are from Cloughton Wyke.

FUTURE WORK. The cone fragments described here were apparently not recognised when collected but only when the surfaces were searched with a microscope. There is thus a reasonable chance that search in a rich bed of *L. falcatus* would yield better specimens. The other chief need is to work out the phyllotaxis in specimens which make satisfactory balsam transfers.

COMPARISON. *L. falcatus* is probably confined to Yorkshire. The only foreign specimen attributed to it is one from Bornholm (Möller, 1902: 62, pl. 6, fig. 21) but this differs in its relatively fewer leaves. There are only about five lateral leaves in all on each segment of the dichotomously branched stem instead of about ten. Its branching is more equally dichotomous than is usual in *L. falcatus*. Lundblad (1950: 12) states that it is heterophyllous.

Specimens of *Selaginellites* and *Lycopodites* described under other specific names are all clearly distinguished. These include:

Selaginella dichotoma Velenovsky (Velenovsky & Viniklar, 1931) Cretaceous of Bohemia. A sterile shoot, differing in its blunt, spreading leaves.

Selaginellites hallei Lundblad (1950) or *Selaginella hallei* Lundblad (1950a). Rhaetic of Sweden. A heterosporous cone and shoot with heterophyllous leaves, more crowded than in *L. falcatus*.

Selaginella nosikovii Kryshstofovich & Prinada (1932). A sterile shoot from the Jurassic of Siberia. The leaves spread more widely than in *L. falcatus*.

Selaginella renaulti Nathorst (1886). Rhaetic of Sweden. Identified with *L. scanicus* by Lundblad (1950).

Selaginellites polaris Lundblad (1949). Trias of Greenland. A heterosporous cone.

Lycopodites arberi Edwards (1934). Jurassic of New Zealand. Isophyllous?, the leaves differ in their contracted bases from *L. falcatus*.

Lycopodites gracilis (Morris) Seward & Sahni (1920). Jurassic of India. A heterophyllous shoot, phyllotaxis and contracted leaf bases as in *Selaginella*.

Lycopodites scanicus Nathorst, see Lundblad (1950). A Rhaetic *Selaginella*-like shoot, leaves shorter than in *L. falcatus*.

Lycopodites sewardi Nathorst (1897). Upper Jurassic or Lower Cretaceous of Spitzbergen. The leaves are minute and appressed to the stem.

Lycopodites sp. Halle (1907), Lundblad (1950). Rhaetic of Sweden. The leaves are minute.

Lycopodites teilhardti Seward (1913). English Wealden. A heterophyllous shoot differing from *L. falcatus* in its distant, obtuse leaves.

Lycopodites victoriae Seward (1904a). Jurassic of Victoria, Australia. Like *L. falcatus* but three times as large.

Form Genus TRILETES Reinsch, 1881:50

Definition of Triletes (as used here)

Isolated cutinised spore, diameter exceeding 150 μ . Body of spore rounded, wall showing three radiating cracks separating three equal contact faces.

It is presumed that the spores in question are megaspores and also that they belong to the Lycopodiales, but none of the species described here can be related to its plant of origin. There is, however, a little information about four of them. *T. sparassis* apparently had spores in separate tetrads ripening in sequence (as in *Selaginella*). A few isolated tetrads of *T. onodios* are known and one of *T. murrayi* which may therefore be similar. On the other hand *T.*

phyllicus has been found in large groups in a cutinised sporangium and this suggests *Lepidodendron* or *Isoetes*. The other spores are only known as isolated specimens.

The megaspores of the Yorkshire Deltaics have been collected fairly thoroughly having been found so far in about 350 macerations out of a total of perhaps 1000 (only half of which yielded determinable plants).

The *Triletes* spores occur scattered through the rock substance in moderate numbers in most plant-bearing localities, but they are never present as an important ingredient as in some Carboniferous coals. They probably represent the spores of terrestrial or epiphytic Lycopods which grew at some distance from the swamps and pools and were only washed into the rivers by occasional floods, but I do not think they represent a really distant inland flora, growing for instance in the mountains, otherwise the spore composition of different plant beds should be more uniform than it is.

Triletes species are among the most useful of zone fossils and it was gratifying to find that the Yorkshire Upper Deltaic spore flora corresponds very closely to the spore flora of the Upper Deltaics in the separate basin of the East Midlands.

Megaspores are very easily obtained from the soft Jurassic rocks by maceration; soaking in commercial nitric acid for a long time yields excellent results but the addition of chlorate is apt to damage the cutinised wall. They are best measured dry (or in balsam) but are apt to swell in media containing water. Each species has been studied both dry and in mounts in various media.

In describing spores the mean diameter and also the standard deviation is given, σ , though this figure, followed uncritically, leads to wrong conclusions. The range of size noted is also given because this figure is usually included. Extremes of size is partly a function of the number measured, but is more a matter of luck and of how close is the range of the next species recognised. For other measurements I give the measurements of a 'typical specimen' a subjective concept, but one not far from the mean. The thickness of the spore wall was measured, where possible in a broken specimen.

In general it has been found necessary to figure the spores at a larger magnification than that recommended for Carboniferous ones.

I have not followed Pant (1954) in dividing *Triletes* into several genera because his divisions do not fit the Jurassic spores very well and because it is known that they are likely to be unnatural, as the genus *Selaginella* has spores of widely different types of ornamentation.

Key to Middle Jurassic *Triletes* of Yorkshire and the East Midlands

(Occasional specimens would be misplaced by this key.)

- | | |
|--|--------------------------|
| (1) Arcuate lamellae conspicuous | 2 |
| Arcuate lamellae absent | 5 |
| (2) Spore over 500 μ wide | 3 |
| Spore under 500 μ wide | 4 |
| (3) Wall of spore smooth | <i>T. turbanaeformis</i> |
| Wall of spore wrinkled | <i>T. harrisi</i> |
| (4) Spines weakly developed in all parts | <i>T. richardsoni</i> |
| Spines weak dorsally, strong towards apex | <i>T. phyllicus</i> |
| Spines strong on all parts | <i>T. datura</i> |
| (5) Surfaces netted, but no other appendages | 6 |
| Surfaces not netted, or else netted and with additional appendages | 7 |

(6) Diameter over 1000 μ	<i>T. casses</i>	
Diameter about 600 μ	<i>T. areolatus</i>	
											(and eroded <i>T. sparassis</i>)	
Diameter about 400 μ	<i>T. kendalli</i>	
(7) Diameter over 400 μ	8
Diameter under 400 μ	9
(8) Wall smooth	<i>T. murrayi</i>	
Wall with blunt spines in groups	<i>T. russus</i>	
Wall with curved plates borne on a low net	<i>T. sparassis</i>	
(9) Appendages long, straight, pointed	<i>T. polyskeles</i>	
Appendages long, curved, knobbed	<i>T. corynactis</i>	
Appendages short and blunt	<i>T. onodios</i>	

Triletes richardsoni Murray

Text-fig. 13 A-H

1939 *Triletes richardsoni* Murray, p. 482, text-figs. 9, 10.

EMENDED DIAGNOSIS. Body of spore rounded but vertical height 10–20 per cent. less than the transverse width. Mean transverse width of body 250 μ (550 μ). Dorsal side hemispherical, ventral side forming three large, somewhat flattened facets.

Triradiate lamellae very prominent 30 μ –70 μ high, extending across the whole ventral face and out onto the combined arcuate lamellae. Arcuate lamellae prominent, 30 μ –70 μ high encircling the spore, occasionally better developed opposite the triradiate lamellae to form slight auricles. Triradiate lamellae apparently simple, fairly thick below but thinning to an edge, arcuate lamellae thinner, forming an exceedingly fine edge. Both sets of lamellae showing thick ribs extending from the base to near the edge, and both usually somewhat serrate. Triradiate lamellae often slightly waved from side to side.

Dorsal surface of spore covered with poorly defined ridges of varying development. Ridges forming an irregular net, but meshes of net never well defined or regular in size and shape; where strongly developed, nodes of net often prolonged to form a short simple spine. Surface of facets also covered with ridges but nodes of net more frequently prolonged to form spines, often 15 μ long, occasionally 30 μ long. Spines solid, simple, pointed.

Spore wall not separable into layers on maceration, 8–15 μ thick, texture granular. Ridges and spines formed from its outer layers, spines showing a texture of elongated vesicles. Lamellae showing a texture of conspicuous elongated clear vesicles delimited by a thicker network.

HOLOTYPE. V.26611. Upper Deltaic, Bed 9; Ketton, Rutland.

DISTRIBUTION. Murray lists four Upper Deltaic localities for *T. richardsoni* in the Midlands. It is seldom met in Yorkshire except in the Upper Deltaic where it is locally common. The localities are distributed as follows:

Upper Deltaic	11 locs.
Grey Limestone	2 locs.
Middle Deltaic, Gristhorpe Series	1 loc.
Lower Deltaic	3 locs.

A single specimen is all that is known from each Lower Deltaic locality.

DISCUSSION. The Yorkshire material of *T. richardsoni* agrees perfectly with Murray's description of Midlands material, and the commonest form of Yorkshire spore is like her

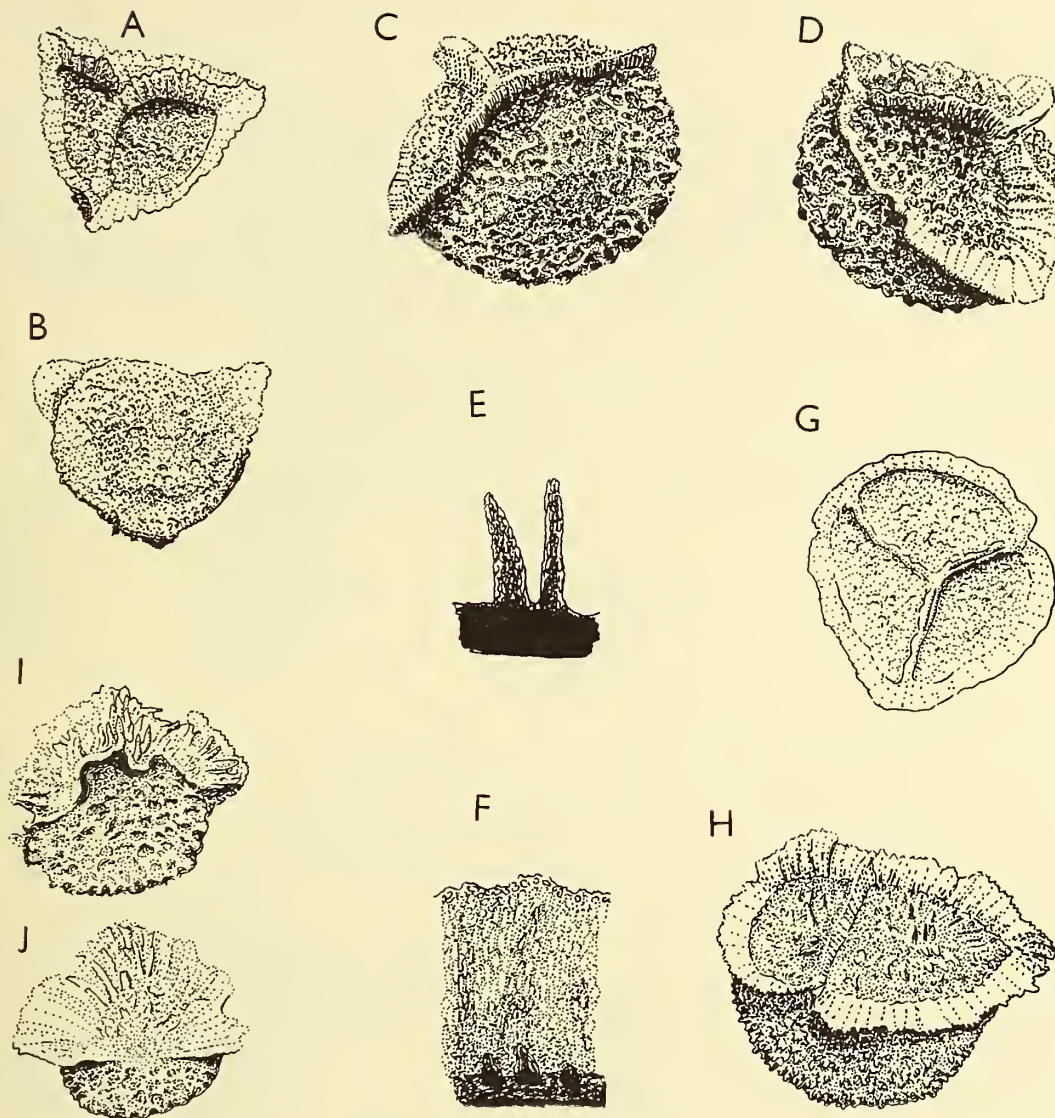


Fig. 13. *Triletes richardsoni* Murray, *T. phyllicus* Murray

A–H, *T. richardsoni*. A, B, small specimen with auricles, surfaces with fine ridges but no spines. V.32640, $\times 100$. C, D, large specimen, dorsal surface with coarse ridges, facets with medium ridges and small spines, V.32641, $\times 100$. E, details of a well-developed spine by transmitted light, V.32642, $\times 500$. F, details of triradiate ridge of same spore by transmitted light, $\times 500$. G, spore with low triradiate and arcuate ridges, facets (and dorsal surface) only faintly reticulate. V.32643, $\times 100$. H, large spore with small spines on dorsal surface and larger ones on facets, V.32644, $\times 100$.

I, J, *T. phyllicus*, small spore with weakly developed appendages, V.32655, $\times 100$.

A–D, H, from Scarborough, White Nab, *Brachyphyllum* Bed. E, F, Black Beck, Loc. 6. G, Osmotherley, Jenny Brewster's Beck, Quarry in Grey Limestone. I, J, Burniston Wyke Beach Bed 1.

figure. The mean width is almost the same (245μ for Yorkshire, 250μ for the Midlands). No spore has been seen as big as Murray's largest; the range of the Yorkshire material being 165μ – 395μ .

Selected specimens have been figured to show most of the range of variation. Text-fig. 13 A is a spore with rather coarse ridges on the dorsal surface, finer ridges and a few minute spines on the facets. Text-fig. 13 B is a small spore with distinct auricles. The ridges on the surfaces are all small and there are no spines. Text-fig. 13 C shows small spines on the dorsal surface and fairly large ones on the facets; the lamellae are serrate. Text-fig. 13 D has remarkably small ridges on its surfaces and the lamellae are narrow and entire. This variation is met in all the larger samples and thus appears to have no taxonomic significance.

COMPARISON. *T. richardsoni* is close to *T. phyllicus*, see below. It is rather less like some zonate Cretaceous spores *T. borealis* Miner (1932), *T. undulatus* Dijkstra (1951) and *T. affinis* Dijkstra. In the Rhaeto-Liassic there are *T. ales* Harris (1935) and *Lycostrobus scotti* Nathorst which also show some points of agreement but they are perhaps nearer *T. phyllicus*.

Triletes phyllicus Murray

Text-figs. 13 I, J; 14

1939 *Triletes phyllicus* Murray, p. 482, text-figs. 7, 8.

EMENDED DIAGNOSIS. Body of spore almost spherical or vertical height 10 per cent less than transverse width. Width of body averaging 260μ , σ 32μ . (Extremes noted among 58 spores measured 180μ and 320μ .) Dorsal side hemispherical, ventral side forming three slightly flattened facets. Triradiate lamellae very prominent, typically 100μ high, extending across the whole ventral face and out onto the arcuate lamellae.

Triradiate lamellae double, substance very delicate, margin waved, surface irregularly ribbed and usually bearing some appendages. Arcuate lamellae forming well developed auricles but reduced in height between the auricles to a small ridge. Arcuate lamellae without appendages but somewhat ribbed.

Dorsal surface of spore covered with well defined ridges forming a rather irregular mesh. Occasional nodes of net prolonged to form a short, simple spine. Surface of facets also showing an irregular net, but net less distinct and bearing larger spines. Spines most strongly developed near the apices of the facets where they form appendages nearly 100μ long. Appendages simple, or forked, straight or curved, usually arising near the triradiate lamellae and sometimes connected with the lamellae.

Spore wall typically about 10μ – 15μ thick, not separating into two layers on maceration. Appendages continuous with the substance of the wall. Fine texture of the wall vesicular. Spines showing elongated vesicles below, more rounded vesicles at their ends; lamellae forming a network separating rounded vesicles about 1μ – 2μ wide.

HOLOTYPE. V.26606. Upper Deltaic, Bed 9; Ketton, Rutland.

DISTRIBUTION. *T. phyllicus* occurs throughout the Deltaic Series and is certainly commoner than its localities indicate, as it is so small and delicate as to be easily missed. It is relatively commonest in the Upper Deltaic where it is sometimes the chief species in an otherwise barren clay. The localities are distributed as follows:

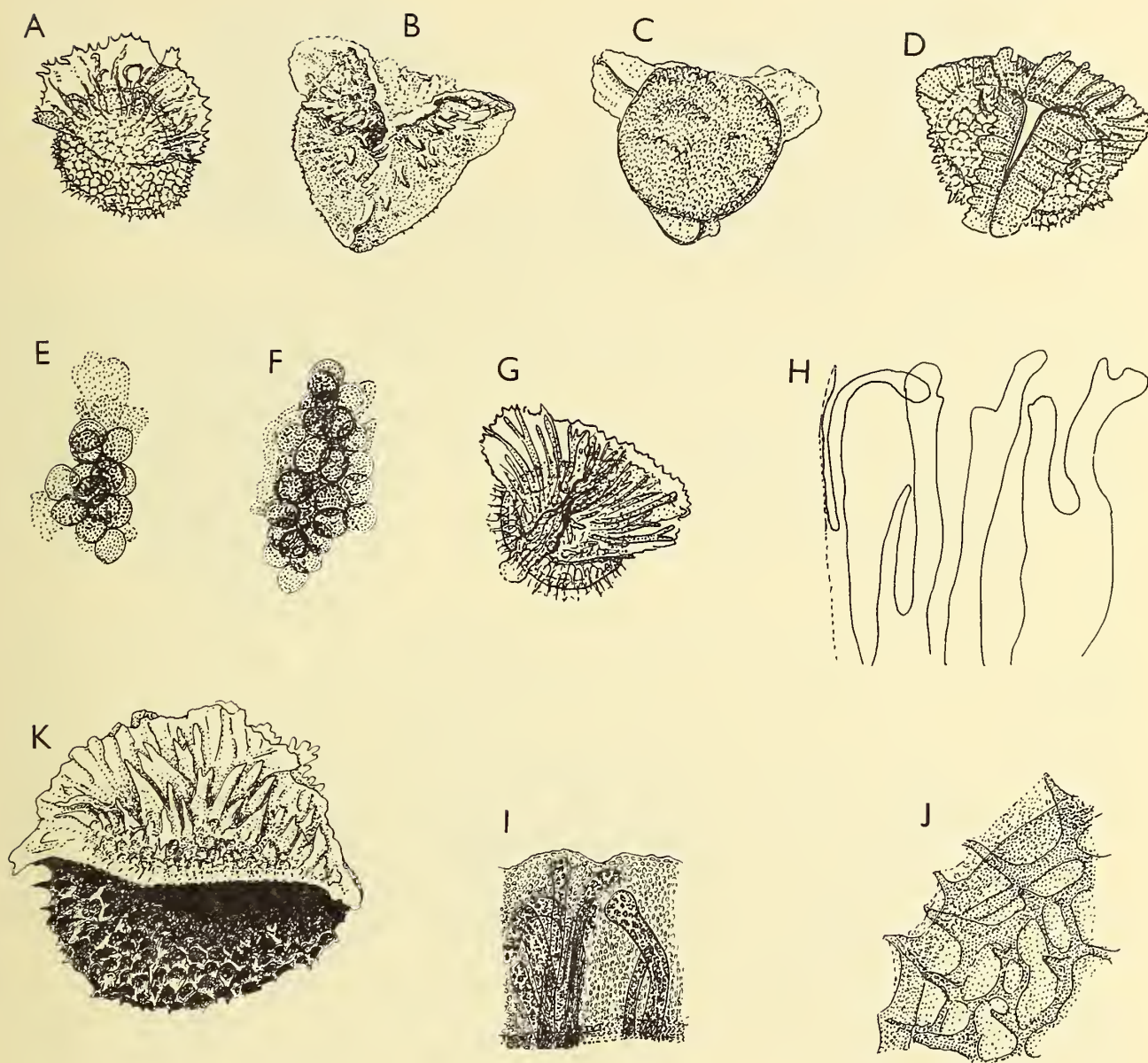


Fig. 14. *Triletes phyllicus* Murray

A, small spore, V.32656, $\times 100$. B, C, larger spore with rather small triradiate ridges, V.32657, $\times 100$. D, spore showing dehiscence, V.32658, $\times 100$. E, F, two groups of spores from one maceration (about 11 and about 25) adhering to a membrane, V.32659, V.32660, $\times 20$. G, small spore with well-developed appendages, V.32656, $\times 100$. H, well-developed appendages (that on the left attached to a triradiate ridge), V.32661, $\times 500$. I, details of rather small triradiate ridge and appendages, V.32656, $\times 500$. J, pits on the dorsal surface of the same spore as I, $\times 500$. K, Giant form from Gristhorpe, Kendall's Cliff Foot Bed, V.32662, $\times 100$. A, G, I, J, Scalby Road Brick pit, Black Clay. B, C, Burniston Wyke, Beach Bed 1. D, Ouse Gill, Black Clay. E, F, Bilsdale, Todhill Beck, Rosy Dykes Coalpits. H, Scalby Wyke, ? Drifted Plant Bed.

Upper Deltaic	5 locs.
Middle Deltaic Gristhorpe Series	15 locs.
Millepore Bed	1 loc.
Middle Deltaic Sycarham Series	7 locs.
Hydraulic Limestone	1 loc.
Lower Deltaic	26 locs.

DISCUSSION. The present specimens which are very numerous form a well defined group and agree perfectly with the specimens described by Murray from the Midlands, except that Murray's material included some larger spores as mentioned below.

A new fact is that these spores are produced in large numbers in cutinised sporangia and not as in *Selaginella*. In one maceration of a coal from Bilsdale, Todhill Beck, Rosy Dykes Coalpit where this species was exceptionally numerous, several fragments of membrane were seen to which these megaspores were adherent; the two best are figured (Text-fig. 14 E, F) and one shows at least 25 megaspores. I presume the coal contained a cone, or at least an intact ripe sporangium and that these sporangia were more like those of *Lepidostrobus* than *Selaginella*. This maceration was exceptional and as a rule *T. phyllicus* spores lie isolated. Later collected material (1956) yielded no further spore masses.

T. phyllicus is rather like *T. richardsoni* but the two are distinguished by the following characters:

In *T. phyllicus* the triradiate lamellae usually stand higher, they are conspicuously double instead of apparently single; their surface bears appendages and its texture is more finely vesicular, but is less distinctly and regularly striated. The appendages are longer and often forked instead of simple and better developed towards the apex of the facets instead of in the middle. The dorsal surface of the spore has better defined ridges and always appears clearly reticulate by transmitted light instead of vaguely marked. In *T. richardsoni* the arcuate lamellae form an equatorial lamella just as high as the triradiate lamellae but in *T. phyllicus* it is only high opposite the triradiate lamellae and dies away between to a slight ridge.

It is also similar to *T. ales* from the Lower Lias of E. Greenland (Harris, 1935) but its triradiate lamellae are lower and its arcuate lamellae rather higher and more conspicuous. The dorsal surface is more spiny and less clearly reticulate.

T. borealis Miner (1932) from the Cretaceous of Greenland is rather similar but has no spines on the facets. The Wealden spores described by Mädler (1954) as *Thomsonia thörensis*, *T. pseudotenella* (Dijkstra) and *T. reticulatus* are all similar to forms of *T. phyllicus*. Their finer details are not known.

Triletes phyllicus Giant form

(or possibly distinct species.)

Text-fig. 14 K

Two Upper Deltaic clays yielded spores (V.32662-64) which look exactly like *T. phyllicus* except that they are nearly twice as large. The width of the body of these spores ranges from 320μ - 500μ . Certain of Murray's slides from the Upper Deltaic clays of the East Midlands, e.g. V.26620a, have also spores of this large size. The appendages of these large spores are larger than those of the small ones, the increase is sometimes almost in proportion, but some-

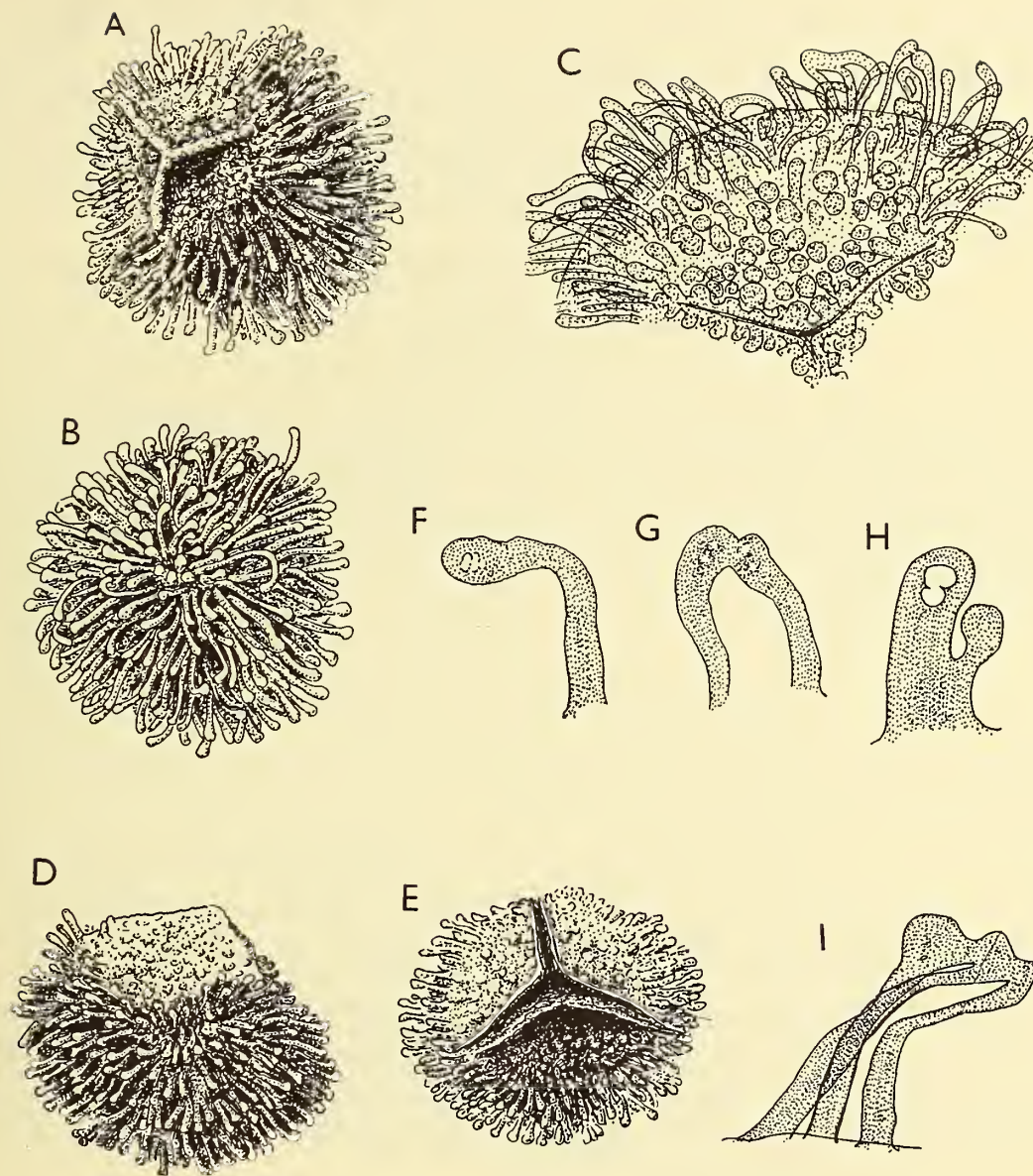


Fig. 15. *Triletes corynactis* sp. nov.

A, B, two sides of holotype, V.32716, $\times 100$. C, specimen by transmitted light, V.32717, $\times 200$. D, specimen in side view (the opposite side is similar), V.32718, $\times 100$. E, specimen with open triradiate lamellae. V.32719, $\times 100$. F–I, appendages, all by transmitted light, $\times 400$. F, commonest form, V.32720. G, simple arch, V.32717. H, unusual form, V.32720. I, triple arch, V.32720.

A, B, D, E are from Cloughton *quinqueloba* Bed. C, G, Gristhorpe, Yons Nab Marine Bed. F, H, I, Osmotherley, Slape Stones Beck, Jet pits.

times there are more meshes across the dorsal side and more of the strap-like outgrowths on the facets.

As these large spores differ in no important respect save size, they are not described as a distinct species. It is clear, however, that we are not here dealing with ordinary fluctuating variation, for among hundreds of specimens of *T. phyllicus* from certain rich localities, none exceeds the normal maximum of 320μ ; while in these other localities every one of the spores found is 320μ wide or over.

Triletes corynactis sp. nov.

Text-fig. 15

DIAGNOSIS. Body of spore almost spherical. Mean width of body excluding appendages, 380μ , σ 50μ ; largest and smallest 480μ and 310μ . Triradiate lamellae prominent, typically 20μ – 30μ high, straight, ending before the margin. Edge of lamella usually appearing single (occasionally divided), blunt, rough but not jagged, surface more or less tuberculate. Arcuate lamellae absent. Contact facets not delimited from rest of spore but distinguished by their short rounded or irregular solid tubercles of varying size. Remainder of spore surface rather thickly covered with long appendages. Appendages typically about 60μ long with a stalk about 8μ thick ending in a rounded head, and occasionally obtuse and not enlarged but never tapered to a point. Appendages sometimes straight but more commonly curved or bent back. Stalks of appendages rarely branched, but appendages united in groups of two or three by their heads to form arches, these arches being evenly distributed over the dorsal surface. Spore wall between the tubercles and between the appendages smooth.

Spore wall 10μ – 15μ thick, not separable into layers. Substance of wall finely granular, substance of appendages composed of rather fine granules separating minute and indistinct lacunae; heads of appendages usually showing one or more large lacunae.

HOLOTYPE. V.32716 (Text-fig. 15 A, B).

DISTRIBUTION. Though *T. corynactis* is common at a few points, its distribution is peculiar in that it occurs as a rare element (about one specimen per kilogram of coal or shale) in a considerable number of localities. No doubt more thorough search would have yielded it in many more samples. It is relatively commoner in the Upper and Middle Deltaic Series than it is below. The localities are distributed as follows:

Upper Deltaic	12 locs.
Grey Limestone	1 loc.
Middle Deltaic Gristhorpe Series	28 locs.
Millepore Series (Yons Nab Marine Series)	1 loc.
Middle Deltaic Sycarham Series	10 locs.
Hydraulic Limestone (Eller Beck Bed)	1 loc.
Lower Deltaic	6 locs.

COMPARISON. The most similar spores are *T. polyskeles* Murray from rocks of the same age in the Midlands (but not Yorkshire) and *T. datura* from the Yorkshire Deltaics. *T. corynactis* is well distinguished from both by its round-headed, not pointed, appendages which differ also in being usually curved and often united to form arches. *T. polyskeles* has also rather

lower triradiate ridges, while *T. datura* has much longer triradiate ridges and a reticulate spore surface.

The name is from *Corynactis*, an anthozoan with knobbed tentacles.

Triletes onodios sp. nov.

Text-figs. 16 I-L; 17 A-E

DIAGNOSIS. Body of spore rounded, only slightly flattened ventrally. Mean width of body 320μ (σ 50μ). Range noted 210μ – 450μ . Contact facets scarcely flattened.

Triradiate lamellae prominent, 40μ – 70μ high. Arcuate lamellae absent, auricles absent. Triradiate lamellae fairly thick below, free edge serrate, sides ribbed. Surface of spore bearing appendages consisting of blunt tubercles or short rods with blunt swollen ends. Appendages usually rather shorter on the facets than on the dorsal surface, appendages often rather flattened in section. Appendages usually separate but occasionally when very well developed forming arches. Surface of spore between appendages without ridges or pits, bases of appendages often irregular but never buttressed. Spore wall not separable into layers on maceration, 10μ thick, texture coarsely granular. Appendages also coarsely granular, not showing any large vesicles.

HOLOTYPE. V.32765 (Text-fig. 16 J, K).

DISTRIBUTION. The distribution of *T. onodios* is interesting, and is as follows:

Upper Deltaic	1 loc.
	(with possibly derived fossils)	
Middle Deltaic Gristhorpe Series	4 locs.
Middle Deltaic Sycarham Series	2 locs.
Lower Deltaic	35 locs.

It is thus one of the more characteristic Lower Deltaic species. This is equally true of the form with long and the form with short appendages.

Its occurrence is in marked contrast with that of *T. corynactis*, for it is often locally abundant and in two localities perfect tetrads of ripe spores were found.

It occurs also in great abundance in a Lower Estuarine clay dredged from the bottom of the River Nene at Wansford, Peterborough, Huntingdonshire (NGR.077994) by Mr. J. L. Gilbert.

DISCUSSION. *T. onodios* varies a good deal in its appendages and an attempt was made to separate it into two species. It is so common at several points that one obtains large spore populations and it was obvious that these populations differed from one another. Thus at Mountain Ash Farm (Text-fig. 16) nearly all the spores have small tubercles and only a very few have short rods. The other extreme is seen at Jack Ass Trod (Text-fig. 17) where nearly all have long knobbed rods and small tubercles are quite exceptional: the ranges in the two localities overlap, it is the means not the ranges which are different. At other localities the spore population appears to be intermediate and whatever the cause of this difference between certain populations it would be unpractical to use it to divide *T. onodios* into two species. Similar variation was noted in mean size, for example at Percy Cross (Text-fig. 17) most of the spores are well over 320μ wide, while at Mountain Ash Farm most are under. The smallest spore at Percy Cross is, however, only 210μ wide.

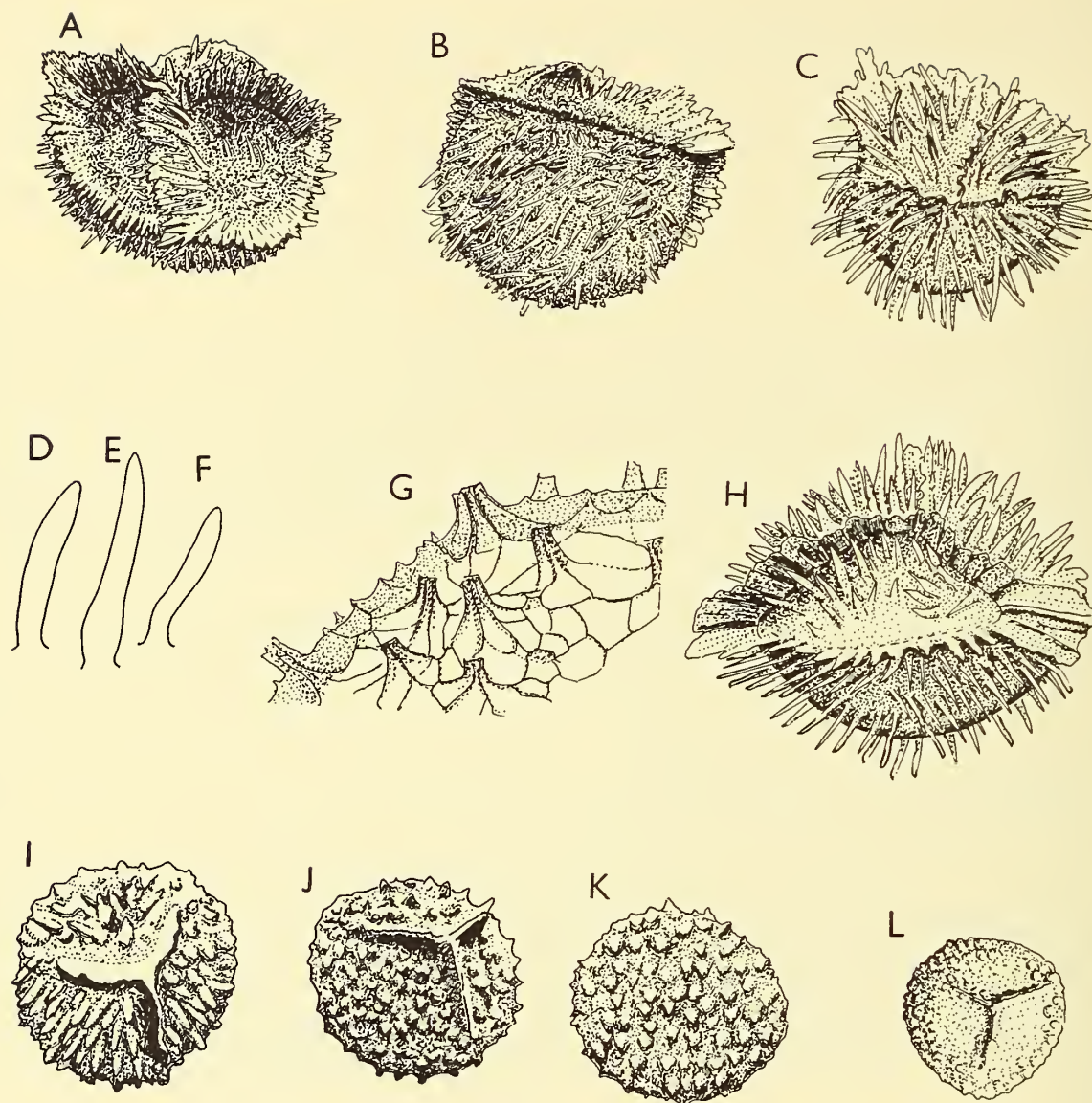


Fig. 16. *Triletes datura* sp. nov.; *T. onodios* sp. nov.

A-H, *T. datura*. A, B, holotype from nearly opposite sides, V.32809, $\times 100$. C, small specimen, V.32810, $\times 100$. D, E, appendages from the specimen in C, $\times 400$. F, appendage from the specimen in G, $\times 400$. G, edge of spore by transmitted light, the appendages are all broken, V.32811, $\times 400$. H, large spore with distinct auricles, V.32809, $\times 100$.

I-L, *T. onodios*. I, specimen with rather long appendages, V.32765, $\times 100$. J, K, holotype from two aspects, V.32765, $\times 100$. L, unusually small specimen with small appendages, V.32765, $\times 100$.

A, B, H, are from Shutt Wood, Kirby Knowle. C, D, E, Spittal Beck, Whitby. F, G, Fryup Dale Coalpits. I-L, Roadside gully, Glaizedale, Mountain Ash Farm.

COMPARISON. Forms of *T. onodios* with long appendages are very near *T. corynactis*. They usually differ, however, in their thicker rods with a more coarsely granular substance and non-vacuolate heads, and the more prominent and more serrate triradiate ridges. Forms with low, tuberculate appendages look very unlike *T. corynactis* but approach the Rhaetic *T. tylotus* Harris. They are distinguished by their separate (not grouped) tubercles and shorter triradiate lamellae.

The name refers to the Jack Ass Trod, one of its localities.

Triletes datura sp. nov.

Text-fig. 16 A-H

DIAGNOSIS. Body of spore rounded but ventral side flat. Mean width of body 340μ (extremes noted 260μ and 375μ). Triradiate lamellae prominent, especially in their outer parts, extending to beyond the edge of the spore, typically 50μ high, forming very delicate plates with a serrated edge best developed at their outer ends. Arcuate lamellae present, almost equatorial in position, lower and stouter than the triradiate lamellae, edge serrate or spiny, surface strongly ribbed. Contact facets rather large, bearing long pointed appendages like those on dorsal side of spore or rather larger. Dorsal side of spore bearing a moderate number of appendages about 80μ long, usually straight, simple, tapering to an acute or obtuse point, never capitate nor united at their ends but occasionally dividing into several branches at the top. Bases of appendages formed by 6-10 buttresses, buttresses running out over spore wall as ridges forming a reticulum, ridges either running to another appendage or forming nodes with only slightly raised points; similar ridges forming the striations on the arcuate lamellae. Spore wall about 10μ - 15μ thick, not separable into two layers, substance very finely and indistinctly granular. Appendages showing only very minute and indistinct vesicles, triradiate lamellae almost homogeneous.

HOLOTYPE. V.32809 (Text-fig. 16 A, B).

DISTRIBUTION. *T. datura* is a rare spore having only seven localities in the Middle Deltaic Gristhorpe Series and one each in the Upper and Lower Deltaic; it is rare in all but one, the coal seam in Kirby Knowle Shutt Wood. Only seventeen specimens have been seen.

On re-examination of Murray's material, a specimen of *T. datura* was found in slide no. V.26610 of *T. phyllicus* from an Upper Deltaic Clay of the East Midlands.

COMPARISON. *T. datura* is apparently fairly constant. The most similar species are *T. polyskeles* Murray which differs in its much smaller triradiate lamellae and the absence of arcuate lamellae, *T. phyllicus* with a different reticulation, shorter spines and more coarsely vesicular structure, and *T. corynactis* with capitate appendages, shorter lamellae and non-reticulate wall.

Triletes russus sp. nov.

Text-fig. 17 F-J

DIAGNOSIS. Body of spore rounded but contact facets flattened or slightly sunken. Mean width of body 500μ , σ 90μ , extremes noted 710μ and 370μ .

Triradiate lamellae not prominent, about 20μ high, length about 0.6 of the spore radius, rather thick, edge not markedly serrate but margins unevenly thickened. Arcuate lamellae absent.

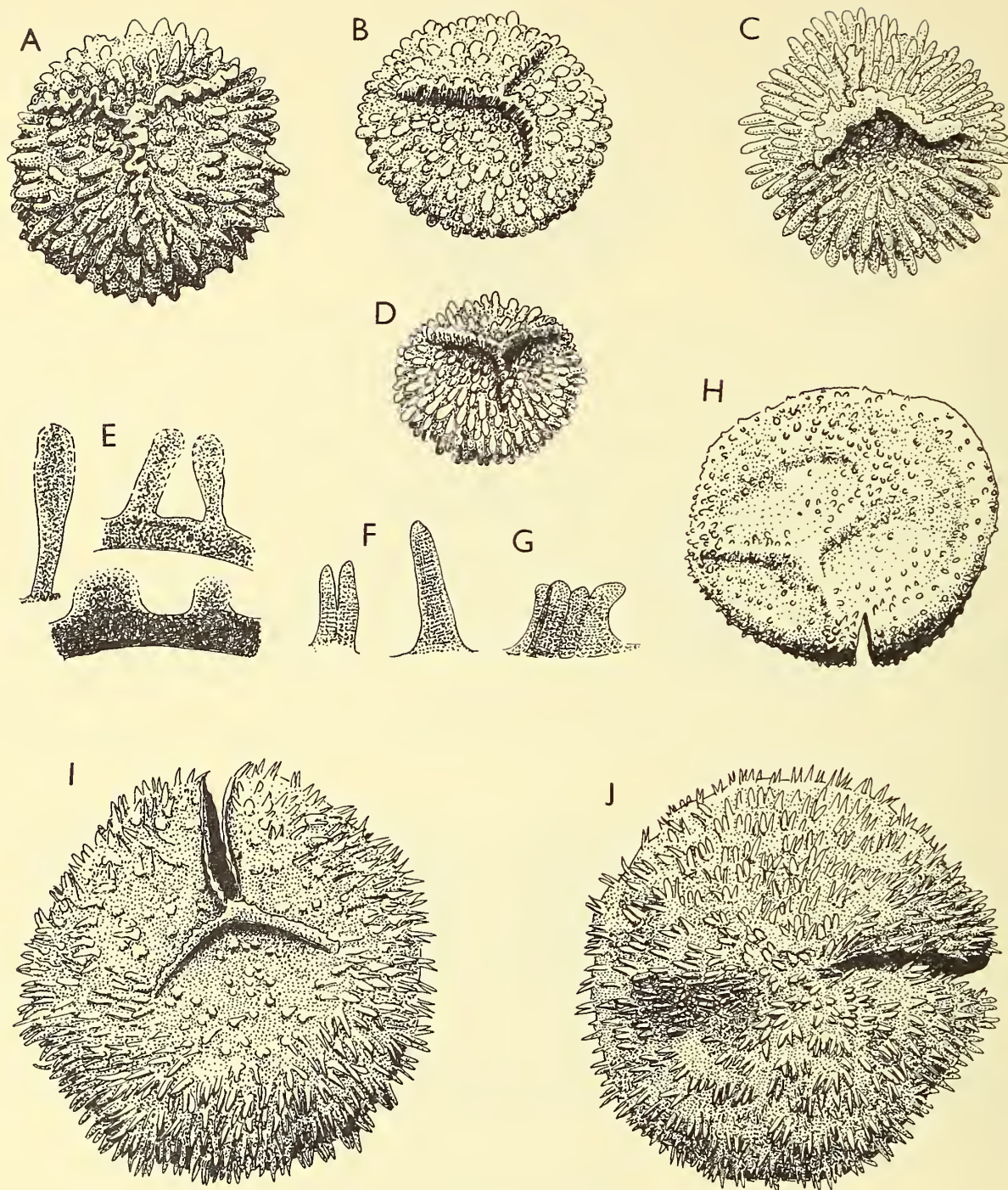


Fig. 17. *Triletes onodios* sp. nov., *T. russus* sp. nov.

A–E, *T. onodios*. A, largest specimen seen, V.32767, $\times 100$. Kildale Percy Cross. B–E, spores of the Jack Ass Trod population, V.32768, $\times 100$. B, smoother specimen; C, rougher specimen; D, exceptionally small specimen. E, appendages of different spores by transmitted light, V.32769, $\times 400$.

F–J, *T. russus*. F, G, appendages of a single spore by transmitted light showing their tendency to be grouped and to show transverse striation, V.32817, $\times 400$. H, unusually smooth specimen, V.32818, $\times 100$. I, J, holotype from two aspects, V.32816, $\times 100$. All the complete spores are dry. F, G, are from R. Rye Bed 4, Snilesworth. H, Damholm Coalpits, Goathland. I, J, Blow Gill Bed 2, Snilesworth.

Surface of whole spore rather sparsely covered with short pointed appendages, appendages on the contact facets rather fewer than on the rest of the spore surface. Appendages conical, straight, two or more often arising close together or partly united in groups; usually of a dark red colour. Substance of appendages very finely granular not vacuolate, granules tending to form very fine transverse striations. Spore wall about 10μ thick, surface between appendages not reticulate or pitted but sometimes bearing a few smaller appendages. Substance of wall coarsely granular, wall not separating into two layers.

HOLOTYPE. V.32816 (Text-fig. 17 I, J).

DISTRIBUTION. *T. russus* occurs throughout the Deltaic Series but is commoner in the lower half of the Series. Its localities are distributed as follows:

Upper Deltaic	1 loc.
Middle Deltaic Gristhorpe Series	4 locs.
Millepore Bed	1 loc.
Middle Deltaic Sycarham Series	8 locs.
Hydraulic Limestone (Eller Beck Bed)	1 loc.
Lower Deltaic	7 locs.

DISCUSSION. *T. russus* is an uncommon species having only twenty-two localities, in none of which is it abundant. The number of specimens studied is only 40. The well developed specimens have a noteworthy appearance, caused by the ruby red appendages on the black background of the spore wall; the fine details of the appendages are also characteristic.

COMPARISON. The most similar Yorkshire species is *T. onodios* which, however, is usually distinguished by its smaller size and blunter, single (not grouped) appendages. The appendages of *T. russus* look rather like those of certain Carboniferous spores (e.g. *T. subpilosus*) but the triradiate ridges are very much smaller. There is no very similar species known in the Liasso-Rhaetic or in the Wealden.

The name refers to the dark red colour.

Triletes sparassis Murray

Text-fig. 18 A-D

1939 *Triletes sparassis* Murray, p. 480, text-figs. 3, 4.

1942 *Triletes sparassis* Murray: Kendall, p. 920, text-fig. 1 A, B. (Yorkshire specimen.)

AMENDED DIAGNOSIS. Body of spore nearly spherical, width excluding appendages averaging 530μ , σ 100μ . (This excludes specimens regarded as immature.) Range noted 300μ – 850μ . Triradiate lamellae about two thirds as long as the spore radius consisting of a broad basal ridge and more delicate extensions; extension uneven, rather sinuous, sides buttressed by ridges, total height usually less than 75μ . Arcuate lamellae absent, contact facets not distinguishable. Whole spore surface typically marked with a coarse network of ridges with wide and irregular meshes. Ridges bearing plate or strap like extensions up to 50μ long. Extensions, where continuous always convoluted and with very jagged edges, spore wall typically thick, not usually separating into two layers, but outer layers including the plates readily destroyed by maceration, leaving only the bases of the triradiate lamellae.

HOLOTYPE. V.26603 (figured Murray, 1939, text-figs. 3, 4). Bed 19 (Upper Deltaic); Ketton, Rutland.

DISTRIBUTION. *T. sparassis* is widespread and often abundant. It occurs throughout the Deltaic Series but its relative frequency is greater in the two lower stages. It has been recognised in the following localities:

Upper Deltaic	19 locs.
Middle Deltaic Gristhorpe Series	26 locs.
Millepore Series	3 locs.
Middle Deltaic Sycarham Series	18 locs.
Hydraulic Limestone (Eller Beck Bed)	1 loc.
Lower Deltaic	51 locs.

The numbers would have been much increased if various ill-preserved or abnormal spores had been identified.

DISCUSSION. *Triletes sparassis* proved the most difficult of all species to study as it appears to be very variable. Part of this variation is caused directly by preparation as the oxidative maceration necessary to break up many rocks destroys the appendages. Even cold nitric acid alone soon causes more or less noticeable bleaching and softening and when these changes have proceeded far, the subsequent treatment with alkali causes the whole spore to swell and the appendages stretch out disproportionately to over 100μ long. They become gelatinous and on drying stick to surfaces and are lost as the spore shrinks. A single spore has been figured before and after this treatment.

Some variation probably results from imperfect development, perhaps simple immaturity. Tetrads assigned to *T. sparassis* have been found in five localities. From one of these, a piece of rock yielded a series of nineteen tetrads of spores which range from 280μ – 600μ wide. The larger ones have typical appendages but the smaller ones have thinner walls and feebler appendages, the smallest a granular surface only. It is assumed that loose spores which more or less match those of the tetrads are starved or immature ones of *T. sparassis*.

Incidentally, the occurrence of these perfect tetrads suggests that the spores were produced as in *Selaginella* rather than as in *Lepidostrobus*. It may be that the series of nineteen tetrads represents part of the contents of a single cone but there is nothing to show whether the small tetrads are simply immature, or as is more likely, starved and abortive specimens from the upper part of a cone.

Other variation relates to original differences and though a considerable range is met in one locality the average condition differs greatly from place to place. This variation is summarised:

- (1) The whole outer layer of the spore wall separates as a continuous layer from the inner layers on excessive maceration.
- (2) The average size of the spore is very different in different samples.
- (3) The basal reticulum on the spore wall is closer and more regular.
- (4) The basal reticulum is feebly developed and so are the free appendages.
- (5) The appendages in the region of the contact facets are much better developed than elsewhere.

Any of these variants may represent a distinct species at present confused with *T. sparassis*.

COMPARISON. Many of the present specimens agree well with those from the Upper Estuarines of the E. Midlands. A wider range of variation has however been accepted.

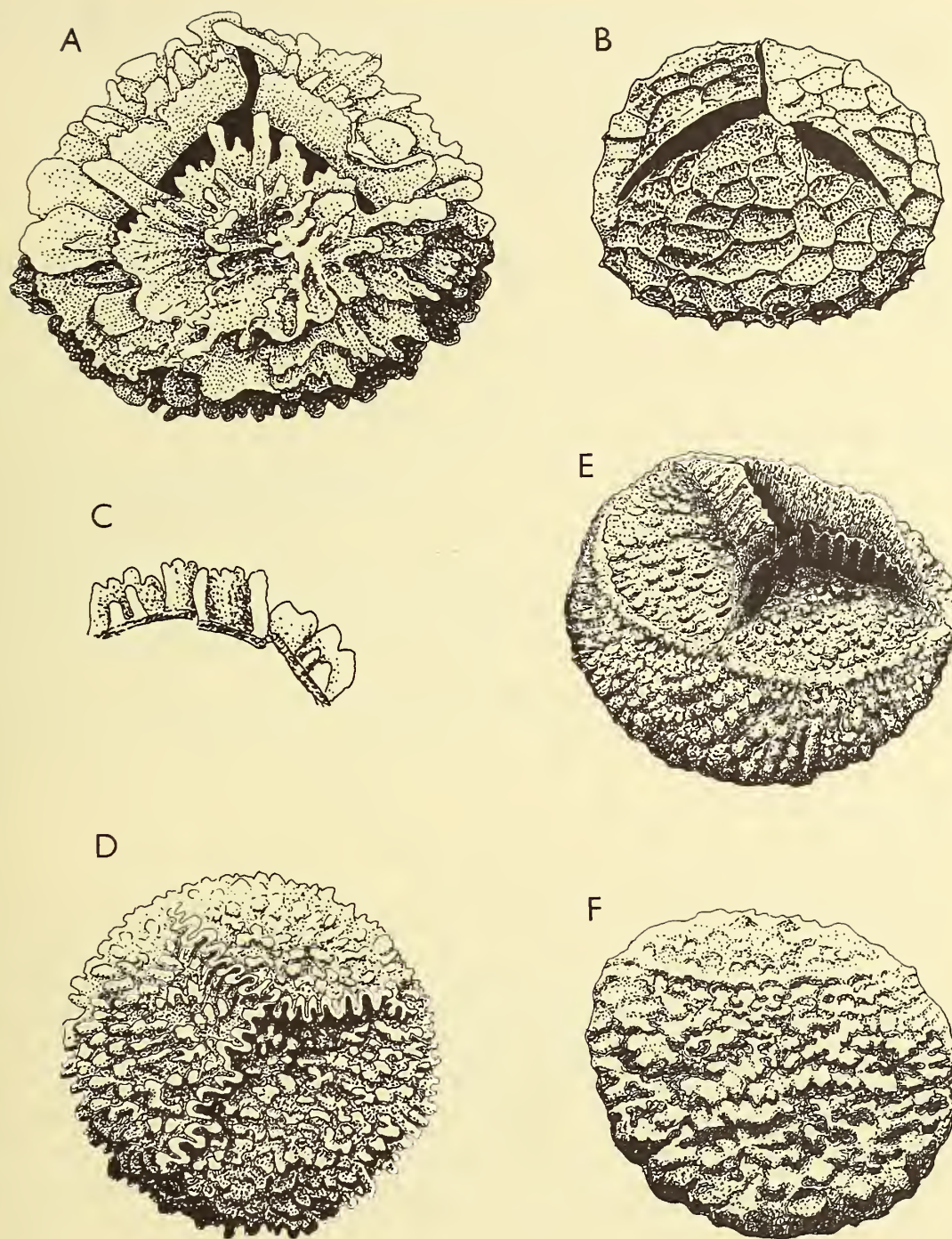


Fig. 18. *Triletes sparassis* Murray, *T. harrisi* Murray

A–D, *T. sparassis*. A, dehiscent spore with well-developed appendages. B, the same spore after further maceration. Specimen subsequently lost. C, wall in section (broken), V.32835. D, specimen with small appendages (the back is similar), V.32835.

E, F, *T. harrisi*, two views of a typical dehiscent specimen, V.32938.

A–D from the Gristhorpe Bed. E, F, Eskdaleside Old Alum Quarry. All $\times 100$.

When partly abraded by maceration the spore looks like *T. harrisi* but it lacks arcuate ridges. Small specimens somewhat resemble the large form of *T. phyllicus* but have a thicker wall and no arcuate ridges.

***Triletes harrisi* Murray**

Text-fig. 18 E, F

1939 *Triletes harrisi* Murray, p. 480, text-figs. 1, 2.

EMENDED DIAGNOSIS. Spore rounded but facets flattened; mean width 600μ (σ 70μ). Range noted 400μ – 690μ .

Triradiate lamellae prominent, up to 60μ high, but diminishing outwards to an indistinct ridge, total length two thirds of the spore radius, inner parts often gaping widely. Lamellae straight, outer surface smooth, edge sharp, entire or waved. Arcuate ridges distinct but without lamellae, surface almost smooth. Auricles absent.

Dorsal surface of spore covered with low irregular tubercles or ridges, or ridges uniting to form a low, coarse network, surface of ridges or network never bearing appendages. Surface of facets bearing smaller tubercles than the dorsal surface with less tendency to form a network. Spore wall a dull black colour, always thick (up to 50μ). Outer layer with ornamentation separable from under layer on prolonged maceration. Substance of wall finely granular.

HOLOTYPE. Specimen figured Murray (1939, text-figs. 1, 2). Bed 18 (Upper Deltaic); Little Bytham, Lincs.

DISTRIBUTION. *T. harrisi* is abundant in certain Lower Deltaic localities but no tetrads were found. Its distribution is as follows:

Upper Deltaic	6 locs.
Grey Limestone	1 loc.
Middle Deltaic Gristhorpe Series	5 locs.
Millepore Bed	1 loc.
Middle Deltaic Sycarham Series	6 locs.
Lower Deltaic	15 locs.

DISCUSSION. Murray's specimens tend to be smaller than those from Yorkshire but the difference is slight. Spores agreeing very closely with Murray's *T. harrisi* are common but there are also a good many which are difficult to separate from *T. sparassis*. It is presumed that most of these difficult specimens were immature, over-macerated or unusual ones of one or other species and they were rejected; the surviving population of *T. harrisi* is accordingly rather uniform and well distinguished from typical *T. sparassis* by possessing distinct arcuate ridges (absent in *T. sparassis*) and in being without any plate-like appendages. In *T. sparassis* also the ridges on the facet region are at least as large as in the rest of the spore; in *T. harrisi* they are nearly always smaller.

***Triletes casses* sp. nov.**

Text-fig. 19 D, F

DIAGNOSIS. Spore spherical, mean width 1300μ , σ 250μ (range 1900μ – 890μ). Triradiate lamellae prominent, up to 60μ high and 40μ broad at the apex but diminishing towards their ends; length two thirds of the spore radius. Triradiate lamellae smooth, straight.

Contact facets scarcely flattened, either not delimited or marked off by a border formed by a regular row of edges of the surface pits; this border occasionally being slightly prominent. Surface of spore marked with conspicuous ridges forming a network with meshes about 70μ broad; ridges about 20μ high and 10μ broad; dying away at the base of the triradiate lamellae. Network on the contact facets similar to the rest of the spore, or average size slightly smaller. Spore wall usually very thick (about 50μ), lined with a thin, detachable membrane. Substance obscurely and irregularly granular.

HOLOTYPE. V.32971 (Text-fig. 19 F).

DISTRIBUTION. *T. casses* ranges throughout the Deltaic Series but most of its localities are in the Lower Deltaic.

Upper Deltaic	2 locs.
Grey Limestone	1 loc.
Middle Deltaic Gristhorpe Series	10 locs.
Millepore Bed and Whitwell Oolite	2 locs.
Middle Deltaic Sycarham Series	4 locs.
Hydraulic Limestone	1 loc.
Lower Deltaic	14 locs.

DISCUSSION. *T. casses* includes the largest spores in the Yorkshire flora and, possibly the largest known Mesozoic megaspores. Well grown specimens are easily recognised and for this reason *T. casses* has been noticed in a fair number of localities, though it is probably one of the rarer species in the flora. It is common at one point only, Whitby West Cliff.

COMPARISON. The only similar spore is *T. areolatus* Harris. Well developed specimens of *T. casses* are larger, thicker walled with a coarser net and higher triradiate ridges.

The name is from *casses* a coarse net.

Triletes areolatus Harris

Text-fig. 19 E

1935 *Triletes areolatus* Harris, p. 158, pl. 26, figs. 3, 10; text-fig. 51 A-F. (Greenland Liassic specimens.)

?1942 *Triletes cyttaria* Kendall, p. 920, text-fig. 1 A, B. (? Abnormal Yorkshire specimen.)

EMENDED DIAGNOSIS. Almost spherical megaspore varying in diameter from 600μ – 1400μ .* Wall not particularly hard, 15μ – 30μ thick, not separable into two layers by maceration. Triradiate lamellae fairly conspicuous, up to 30μ wide, projecting about 15μ ; their length being 0.5–0.7 of the radius of the spore. Arcuate lamellae absent, but occasionally the pits in the wall are so arranged as to give a slight suggestion of a lower border to the 'facets', but in most cases 'facets' entirely undistinguished. Surface of spore marked with more or less conspicuous round or polygonal pits about 30μ wide and up to 15μ deep and separated from adjacent pits by ridges about 5μ broad. Substance of wall showing a fine granular structure.

DISTRIBUTION. *T. areolatus* occurs chiefly in the lower half of the Deltaic Series. Its localities are as follows:

Upper Deltaic	6 locs.
Middle Deltaic Gristhorpe Series	3 locs.
Middle Deltaic Sycarham Series	6 locs.
Hydraulic Limestone	1 loc.
Lower Deltaic	8 locs.

* The Yorkshire specimens average 600μ wide, σ 90μ ; the largest noted was 780μ , the smallest 500μ .

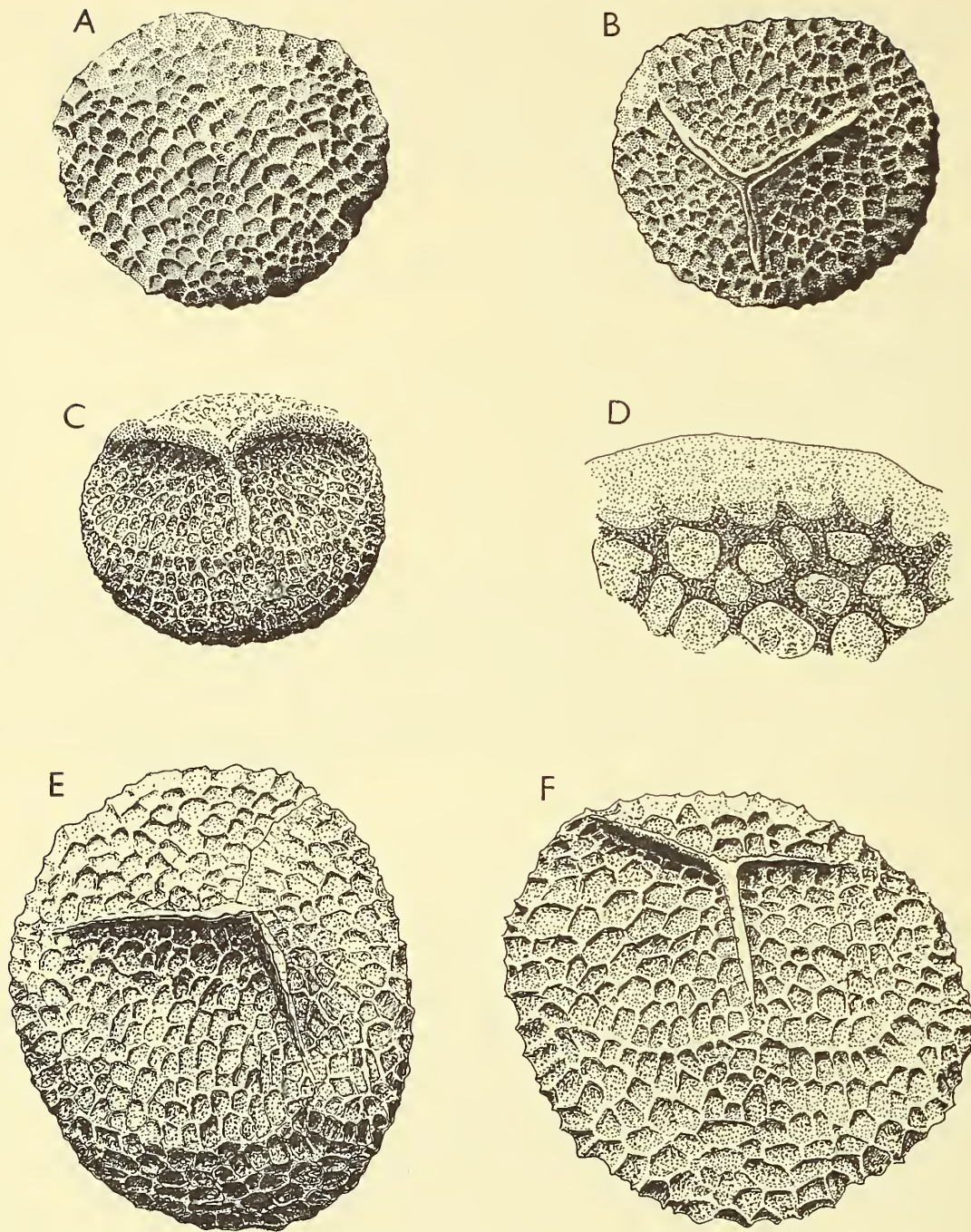


Fig. 19. *Triletes kendalli* sp. nov., *T. casses* sp. nov., *T. areolatus* Harris

A–C, *T. kendalli*. A, B, holotype drawn by Miss M. W. Kendall. The arcuate ridges are indistinguishable, V.33017, $\times 100$. C, specimen with slightly distinguished arcuate ridges but a less distinct reticulum, V.33018, $\times 100$. D, *T. casses*, part of a broken specimen showing the triradiate ridge and reticulation; by transmitted light. V.32970, $\times 100$. E, *T. areolatus* (the dorsal surface is similar), V.32997, $\times 100$. F, *T. casses*, holotype (V.32971) $\times 50$ only; compare E and F.

A, B, from Fryup Dale Head Coalpits. C, Clither Beck Coalpits. D, F, Whitby West Cliff. E, Sandsend Alum pit, loc. A.

DESCRIPTION. The Yorkshire spores agree closely with *T. areolatus* Harris (Lower Lias of E. Greenland) in everything except their smaller average size and lower size range; the Yorkshire spores being indeed remarkably uniform. The Greenland spores were measured in the moist state in glycerine jelly mounts which caused some swelling, especially of any over-macerated specimens, but no doubt their size really was greater. In spite of this they are identified because it is impossible to distinguish most of the specimens.

The wall of the spore is quickly destroyed by over-maceration and even then does not separate into layers. The wall of some of the best preserved spores, however, when broken, shows a delicate inner membrane which is readily torn from the main wall. A number of specimens show collapsed contact facets and a marked bend in the spore wall so as to form a slight arcuate ridge, and a change in the pattern of pitting is often visible just here but there is never any considerable projecting arcuate lamella. The netting on the facets is sometimes elongated (in the radial direction) but isodiametric over the back of the spore. The ridges forming the network are uniformly high and rather broader at the base than at the top. The substance of the wall is finely granular.

COMPARISON. *T. areolatus* differs from *T. harrisi* in its much more regular and better developed net. The Yorkshire material of *T. areolatus* is intermediate in size between *T. casses* and *T. kendalli* and the only differences between the three species besides overall size are in such features as wall thickness and mesh size which may well be related to overall size. It might have been possible indeed to include the specimens of *T. areolatus* among the other two species making them rather more variable. The distribution of the three indicates, however, that they are distinct as they are found, sometimes in great abundance, in different localities where the spore population is rather uniform and includes no typical specimen of the morphologically adjacent species. Where a few specimens or one only is found in a maceration this argument does not of course apply and the specimens are determined according to which mean they approach most nearly.

The spore named *T. cyttaria* Kendall (1942) has more widely spaced pits than any normal specimen of *T. areolatus*, but is perhaps an extreme form. I have found no specimens exactly like it.

***Triletes kendalli* sp. nov.**

Text-fig. 19 A-C

DIAGNOSIS. Spore spherical, mean width 450μ ($\sigma 65\mu$), range noted 320μ – 510μ . Triradiate lamellae fairly prominent, straight, the free edges and surface smooth, length 66–80 per cent of the spore radius, height typically up to 25μ persisting with little diminution to the ends. Arcuate ridges and lamellae absent or at most obscurely marked by a slight ridge and a change in the pattern of surface pits. Contact facets not flattened, usually not distinguishable.

Surface of spore marked with ridges forming rather regular pits typically 25μ broad. Ridges typically 10μ high (rather higher where three meet) thickened below so as to make the pits more or less saucer-shaped. Spore wall thin (typically 15μ in the pits); readily destroyed by maceration but not separating into distinct layers. Surface appearing finely mottled when dry; substance finely and obscurely granular when cleared by maceration.

HOLOTYPE. V.33017 (Text-fig. 19 A, B).

DISTRIBUTION. *T. kendalli* is very common throughout the Middle Deltaic but rare above and below. It occurs in the tip heaps of most of the old coal pits on the moors; these have been reckoned in groups of up to 50 as one locality, but had they been considered separately, the number of Middle Deltaic localities might have exceeded a thousand. Its localities are as follows:

Upper Deltaic	6 locs.
Middle Deltaic Gristhorpe Series	47 locs.
Millepore Series	1 loc.
Middle Deltaic Sycarham Series	15 locs.
Lower Deltaic	6 locs.

The fact that *T. kendalli* is abundant in the Gristhorpe Series and rare in the Upper Deltaic indicates that the material of the Upper Deltaics is not to any great extent derived from the Middle Deltaics but from other sources.

DISCUSSION AND COMPARISON. *T. kendalli* is abundant in many Middle Deltaic coals and many thousands were seen, and the great majority are nearly uniform in size and appearance. The populations in these rich localities agree with one another, and *T. kendalli* is indeed one of the most easily determined and useful zone fossils of the Deltaic Series.

The mean sizes of spores of *T. kendalli* were compared from six Middle Deltaic localities where it is abundant. The results are:

375 μ Gristhorpe Series
445 μ Gristhorpe Series
450 μ Gristhorpe Series
450 μ Sycarham Series
450 μ Sycarham Series
475 μ Gristhorpe Series.

The standard deviations being about 60 μ and the numbers measured being over 20, the extreme differences look significant, but they may result from selection in deposition, sieving, decantation and capture for mounting.

The very few spores of the Upper and Lower Deltaics attributed to *T. kendalli* were also measured (the various localities being taken together). The nine Upper Deltaic spores and the seven Lower Deltaic ones had almost exactly the same mean of 520 μ . I suspect that this larger size is not the result of selection (for these few include the largest spores seen) but indicate a real difference though scarcely one of taxonomic value.

The fossil has been named after Miss Mabel Kendall who drew the type specimen and made notes describing this species.

Triletes murrayi sp. nov.

Text-figs. 20; 21 A, B

1929 '*Selaginellites* sp.', Black, p. 418.

1939 *Triletes* sp. 'A', Murray, p. 484, text-fig. 11.

DIAGNOSIS. Spore nearly spherical, mean width 830 μ , σ 220 μ (range noted 250 μ –1400 μ , those below 500 μ regarded as abortive). In normal spores, triradiate lamellae typically 60 μ broad, 40 μ high, not prominent but sharply defined by a groove 10 μ –20 μ broad along their

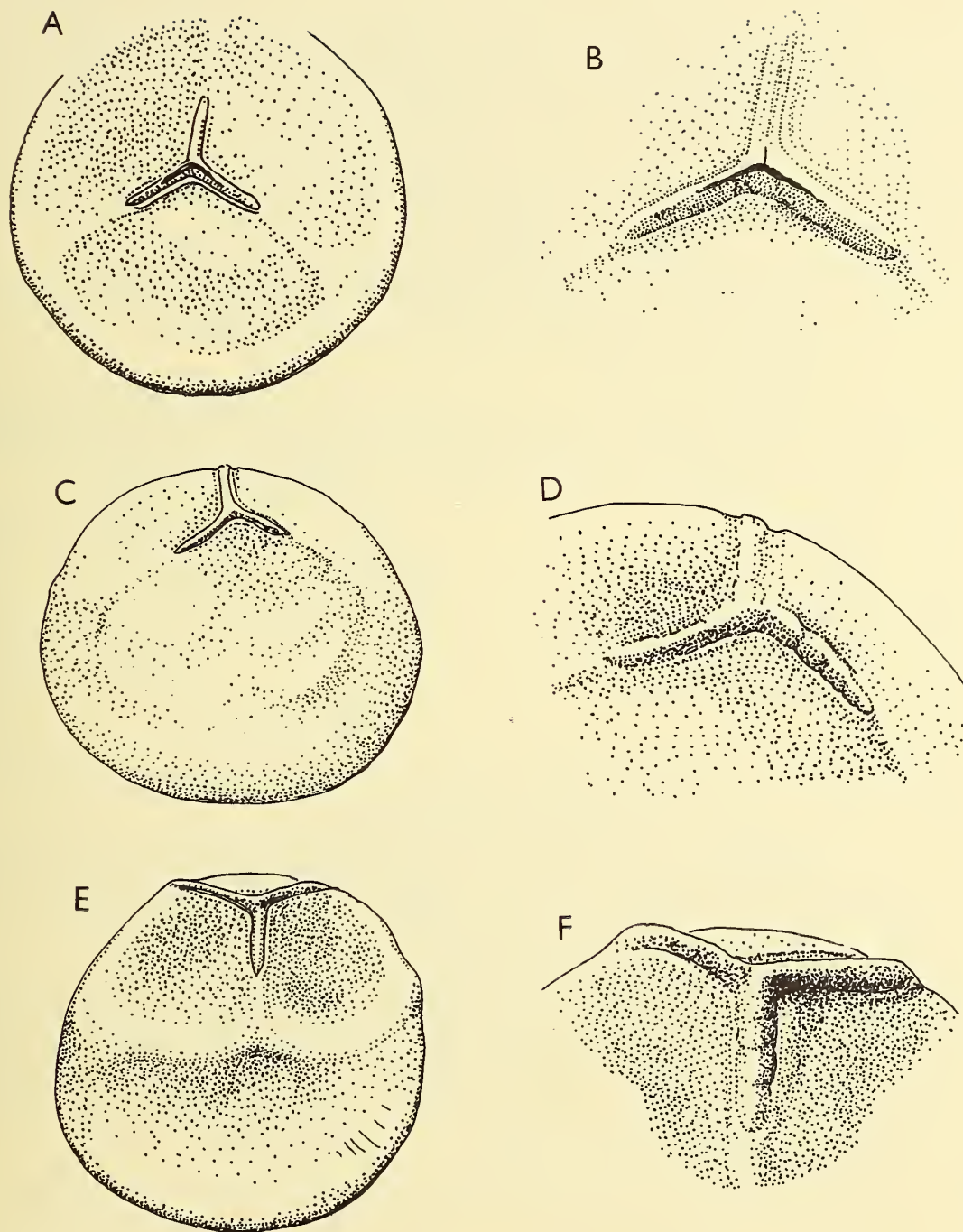


Fig. 20. *Triletes murrayi* sp. nov.

Three spores from the Scalby Wyke Drifted Plant Bed. A, C, E show the whole spores, $\times 50$. B, D, F show the triradiate ridges only, $\times 100$. In E the contact facets have collapsed. V.33082.

edges. Triradiate lamellae very short, length only one-third the spore radius; edge flattened or occasionally showing two or three rounded bulges; triradiate cracks rarely conspicuous.

Contact facets either completely undelimited, or suggested by low and ill-defined folds in the spore wall continuing the triradiate lamellae and then suggesting arcuate ridges; but no true ridges developed. Surface of whole spore wall smooth, polished; wall very thick and rigid (30μ – 50μ thick in broken specimens), substance uniform and finely granular. Inner cutinised membrane present, thin (about 2μ) but tough, more or less adherent to outer spore wall but after long maceration separating from the swollen outer wall and then showing a sculpture of small parallel ridges (? folds caused by crushing).

Smaller spores (regarded as abortive) usually with triradiate ridges nearly as long as in the normal ones and therefore occupying a larger fraction of the spore radius; ridges feebly or not at all delimited by grooves; spore wall thinner than in normal sized spore.

HOLOTYPE. V.33082 (Text-fig. 20).

DISTRIBUTION. *Triletes murrayi* occurs at all levels in the Yorkshire Deltaic Series as well as in the marine intercalations and is often extremely abundant especially in the Upper Deltaic where it is the commonest fossil. Its localities are distributed as follows:

Upper Deltaic	39 locs.
Grey Limestone	1 loc.
Middle Deltaic Gristhorpe Series	25 locs.
Millepore Bed and Whitwell Oolite	4 locs.
Middle Deltaic Sycarham Series	26 locs.
Hydraulic Limestone Series	1 loc.
Lower Deltaic	34 locs.

Its relative rarity in the Gristhorpe Series is due to its absence from any of the numerous coal samples from the coalfield of the moors around Farndale.

DISCUSSION. The range in size of spores attributed to *Triletes murrayi* is unusually great. The whole series were identified because there is full intergradation and because the large, normal and small spores are associated in many localities. A histogram (Text-fig. 21 A) was constructed for the diameter of nearly 300 spores; it is smooth but skew.

This evidence is consistent with the view that the small spores were not a separate category but on the contrary that the cone of *T. murrayi* produced spores showing both the normal variation in size and also a proportion of spores which were starved and aborted at different stages of growth. The possibility that it produced full and abortive megaspores like *Lepidocarpon* was considered but the evidence is against this. Lundblad (1950a) gives a similar histogram for *Triletes pinguis* or *Selaginella hallei*.

Only one rather ill-preserved tetrad of small sized spores of *T. murrayi* was seen.

COMPARISON. The Yorkshire material agrees perfectly with the spores figured and described as *Triletes* sp. A. by Murray (1939). Murray's specimens are from the Upper Estuarine of the English Midlands. Although *T. murrayi* is a smooth-walled spore there seem remarkably few species which agree with it in its short triradiate ridges with a marginal groove. In the Carboniferous a few specimens placed in *Triletes glabratus* and in *T. reinschi* are near it but most are much larger, and differ in having well-defined arcuate ridges. No very similar spore is known in the Liasso-Rhaetic of Greenland or in the Wealden of Holland, though some,

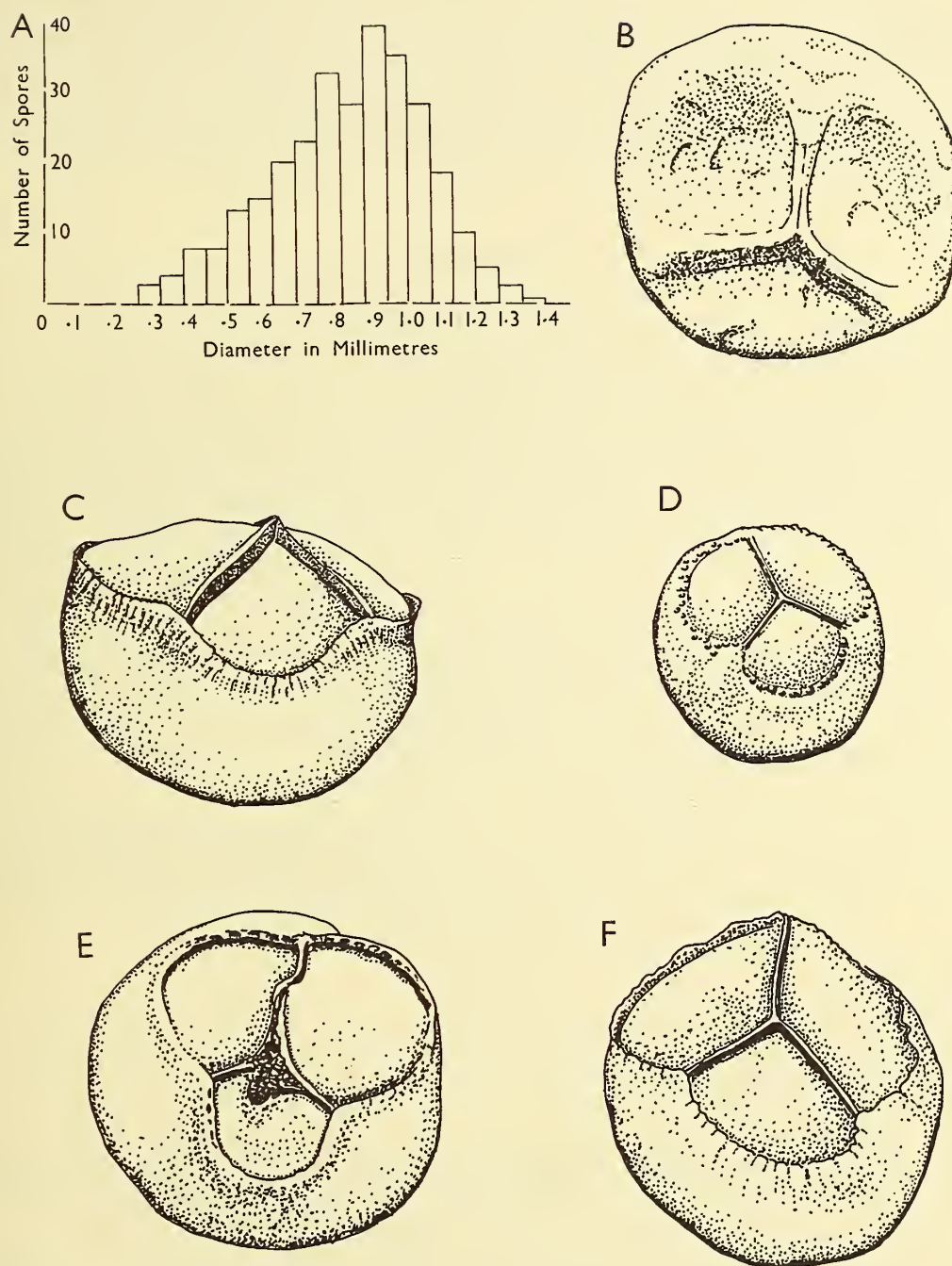


Fig. 21. *Triletes murrayi* sp. nov., *T. turbanaeformis* sp. nov.

A, B, *T. murrayi*. A, histogram giving the diameters of nearly 300 spores. B, spore of small size, V.33084, $\times 100$.

C–F, *T. turbanaeformis*. C, holotype, V.33201, $\times 50$. D, small specimen with low tuberculate ridges, V.33202, $\times 50$. E, specimen showing dehiscence, V.33203, $\times 50$. F, specimen V.33204, $\times 50$.

B, from Snilesworth, Wheat Beck loc. 3. C, Cloughton coal below *quinqueloba* Bed. D, Hutton Mulgrave, Birkhead Beck, loc. Y. E, Danby, Clither Beck Coalpits. F, Goathland Mallyon, Bed 3.

e.g. *Triletes persimilis* Harris, with relatively longer triradiate furrows are like the smaller spores attributed to *T. murrayi*. *T. polaris* Lundblad (1949), a rather smaller Triassic spore, *T. pinguis* (*Selaginella hallei* Lundblad, 1950a) a smaller Rhaetic spore also resemble the smaller spores of *T. murrayi* and have an inner cutinised membrane detachable after maceration. It is thus clear that the full sized spores of *Triletes murrayi* are well characterised but the smaller ones are less determinable.

***Triletes turbanaeformis* sp. nov.**

Text-fig. 21 C-F

DIAGNOSIS. Spore rounded but somewhat flattened ventrally. Mean transverse width of spore 940μ ($\sigma 140\mu$) extremes noted 1260μ and 670μ .

Triradiate lamellae prominent, 40μ high, edge sharp and straight. Length about half the spore radius, extending with little reduction up to the arcuate lamellae. Arcuate lamellae well developed, sometimes especially developed opposite the triradiate lamellae to form slight auricles; edge of arcuate lamella pointing forwards and often concealing the margins of the contact facets, sometimes entire, but more often sinuous or slightly tuberculate. Contact facets usually swollen in the middle but sunken along the triradiate ridge. Dorsal side of spore rounded; facets and dorsal surface of spore almost smooth but made dull and shagreened by innumerable minute pits. Wall very thick (up to 40μ) main part composed of an almost homogeneous substance but becoming finely vesicular after maceration, enclosing a separable inner membrane forming a tough granular sac about 2μ thick.

HOLOTYPE. V.33201 (Text-fig. 21 C).

DISTRIBUTION. It is commonest in the old coalpits at Clitherbeck, Danby where a dozen whole or broken specimens were found; elsewhere it is mostly represented by single specimens. It is, however, rather widely and evenly distributed, the twenty-two localities being as follows:

Upper Deltaic (Moor Grit)	4 locs.
Grey Limestone	1 locs.
Middle Deltaic Gristhorpe Series	7 locs.
Middle Deltaic Sycarham Series	4 locs.
Lower Deltaic	6 locs.

DISCUSSION. *T. turbanaeformis* is represented by about thirty specimens, eighteen of which were perfect enough for measurement. The specimens agree with one another rather closely and those figured cover almost the whole range of form.

It is very well distinguished from the only other smooth megaspore in Yorkshire, *T. murrayi*, by its sharp arcuate ridges and longer triradiate crests, and it does not resemble any Mesozoic spore known to me. It is, however, like the spores of a number of species of *Selaginella* and also certain Carboniferous spores included by Dijkstra (1946) in *T. glabratus* and in *T. fulgens* Zerndt (Type 9 of Zerndt, 1931). None of them, however, agrees perfectly in the sharp triradiate crest and turgid facets.

The name was suggested by its resemblance in shape to the Turk's cap gourd, *Cucurbita pepo turbanaeformis*.

UNDETERMINED SPECIES OF *TRILETES*

Almost all the megaspores met have been placed in one of the previous species or else rejected as immature or ill-preserved. Five well-preserved kinds were, however, noted which could not be fitted into any Jurassic or Carboniferous species, and accordingly are regarded as unknown species, or else very abnormal and unrecognisable specimens of known ones. All these are rare and therefore not described, but the specimens are in the British Museum (Natural History).

DERIVED CARBONIFEROUS SPORES

A few macerations yielded well-known Carboniferous spores in small or sometimes large numbers. The origin of these may be from derived Carboniferous coal fragments, but may also be from Carboniferous coal dust recently dropped by man. All reasonable precautions were taken in collecting samples, but it is impossible to be absolutely sure there is no contamination, all that can be done is to repeat the collecting and maceration. Since the second time I failed to find any Carboniferous spores, I have assumed that the first sample was contaminated, but this reasoning chiefly applies where the first time a good many Carboniferous spores were found.

Genus *ANEULETES* nov.

DIAGNOSIS. Hollow sac of more than 200μ diameter; wall thickly cutinised, not cellular, without any contact furrows or germinal cracks.

This genus is intended for bodies which resemble megaspores in size and structure but have no furrows or cracks. The name *Aletes* is not appropriate because its author (Naumova) made it for microspores.

TYPE SPECIES. *Aneuletes patera* sp. nov.

Aneuletes patera sp. nov.

Text-fig. 22

DIAGNOSIS. Spore, mean diameter 600μ ($\sigma 115\mu$), extremes noted 330μ and 850μ . Shape nearly spherical but with a flat or slightly concave area at one side. Main part of wall smooth apart from innumerable minute pits 2μ wide. Concave area circular in outline, radius one half or two thirds of the radius of the compressed spore, surface showing conspicuous rounded bulges caused by local thickening of the wall. Wall about 10μ thick, very resistant to maceration, not separable into layers by maceration.

HOLOTYPE. V.33220 (Text-fig. 22B).

DISTRIBUTION. *Aneuletes patera* occurs as follows:

Middle Deltaic Gristhorpe Series	4 locs.
Middle Deltaic Sycarham Series	4 locs.
Hydraulic Limestone	1 loc.
Lower Deltaic	7 locs.

It is abundant at Whitby West Cliff (Lower Deltaic), and as the above figures show, becomes rarer in passing up the Deltaic Series. It has not yet been found in the Upper Deltaic.

DISCUSSION. *A. patera* has been found frequently in ordinary macerations of coaly shales, but also occurs in the absence of other plants. A fallen block of grey shale collected by the late W. N. Croft at Whitby showed these spores evenly distributed through it but no other plant (apart from some circles of cellular tissue 1 mm. wide). No other spore has been found in such a manner (before maceration) in the Yorkshire Jurassic.

It has been found impossible to classify *Aneuletes patera*; it does not resemble any known Lycopod megaspore, nor yet the spores of any genus of Hydropterids. The associated plant remains give no help.

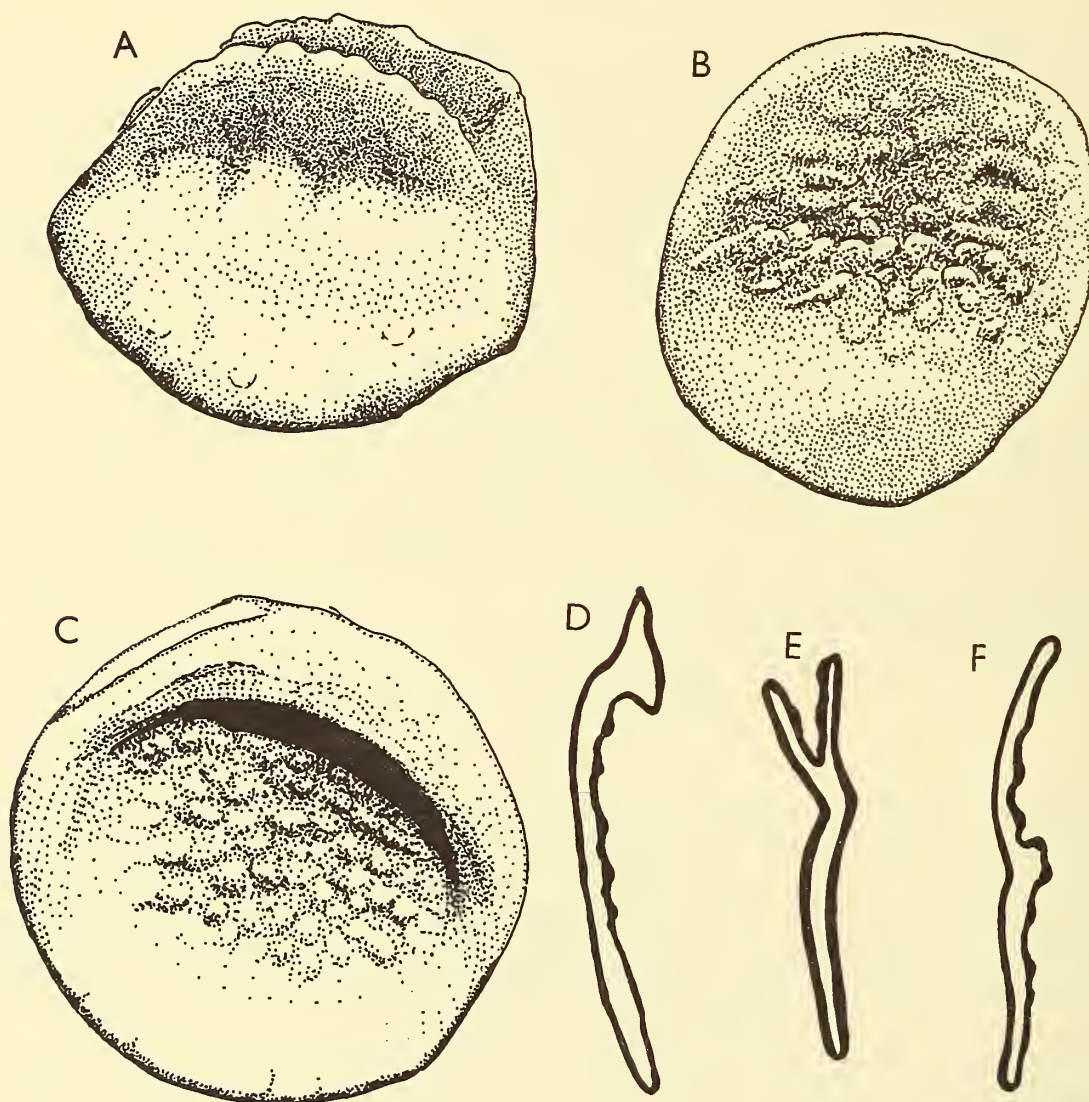


Fig. 22. *Aneuletes patera* sp. nov.

A, specimen with the hollow crushed sideways, V.33221, $\times 100$. B, holotype, the commonest form of crushing, V.33220, $\times 100$. C, specimen in which crushing has produced a fold, V.33220, $\times 100$. D, reconstructed L.S. through C. E, reconstructed L.S. through A. F, reconstructed L.S. through B.

All from Whitby West Cliff.

LARGE CUTINISED SACS

Very many macerations have yielded fragments of cutinised sacs, which when complete are usually oval and about 6 mm. \times 4 mm., but the diameter varies from 2 mm. to about 2 cm. These sacs are composed of a thick and rigid cuticle of a persistently red-brown colour (even when unmacerated they are dark red). They resist maceration very well and so are very easy fossils to find. They have no stratigraphic value for they occur equally commonly at all levels and though varied do not fall into groups resembling species. Indeed, when macerating the Rhaeto-Liassic coals of East Greenland I found great numbers of very similar bodies matching most of those from Yorkshire.

A typical specimen consists of a crushed sac of homogeneous cuticle 30μ thick reinforced on the outside by a network of coarse threads $2-5\mu$ wide which are more or less firmly united to the cutinised sac at occasional points. In some specimens the network is closely united everywhere to the continuous sac. In others it is very ill-developed. In still others the net is robust and found without any sac, but probably a sac was originally present. Specimens both of complete sacs and isolated nets are occasionally to be seen in unmacerated shales and it is perhaps significant that both these sacs and those isolated by maceration show large irregular tears and are full of rock, evidently having been torn when deposited. A curious feature of their distribution is their tendency to occur in small numbers in nearly every rock where cuticles are preserved at all. It is only when a large amount of rock yields them and nothing else that they seem common. This distribution contrasts with all ordinary plant cuticles which are far more uneven, being absent at one point and present in profusion in another.

I am unable to classify these sacs. Had they been found in Carboniferous coals they might have been named as fragments of *Cystosporites* (*Lepidocarpon* spores). Such a determination is impossible, however, because no specimen shows any trace of triradiate scar. It has not been possible to persuade zoologists to recognise them as belonging to their kingdom.

FILICALES

The Filicales are so abundant in the Yorkshire Jurassic flora that they may well have formed the dominant herbs on land, and several species are represented by so many fine specimens that they must have lived conveniently close to the river which presently deposited them.

The number of species here recognised is thirty; this is not very large and is exceeded by several other Jurassic floras. It is low also in proportion to the number of Gymnosperm species. Such figures are, however, misleading. In the first place the number of fern and Gymnosperm species is not comparable because the Gymnosperms are augmented by cuticles from bulk-macerations, but this adds nothing to the ferns. There are thus in effect about 50 available fern localities in Yorkshire and over 500 localities for Gymnosperms.

More important, however, is the fact that fossil species depend on a writer's views, and it seems also as though imperfect knowledge tends to multiply fern species and to diminish Gymnosperms. Thus Phillips (1875) distinguished 44 ferns and Seward rightly reduced these to 15. The additional fifteen species recorded in the present work represent new discoveries.

The distribution of species in families as follows:

Marattiaceae	1
Osmundaceae	5
Matoniaceae	5
Camptopterideae	2
Dipteridaceae	1
Schizaeaceae	2
Dicksoniaceae													
Thyrsopteridae	8
Dicksoniae	2
Aspideae(?)	1
Unclassified	3

In passing from the Lower to the Middle Jurassic the noteworthy changes are the decline in the Camptopterideae and the rise in the Dicksoniaceae. Upper Jurassic ferns are less satisfactorily classified but by the Lower and Middle Cretaceous the Gleicheniaceae rise notably.

Family *MARATTIACEAE*

Genus *MARATTIA* Swartz

This generic name is here used in preference to *Marattiopsis* or *Angiopteridium* for Jurassic fossils thus reviving a practice of a century ago. The fossils agree with this one living genus and with no other. The use of any other name would be purely conventional for there is no known difference of structure. Halle (1921: 2) summarising the position, concluded that *Marattiopsis* may be used 'if we object to referring a Mesozoic plant to a Recent genus'. As pointed out (p. 14) this objection has recently been overruled. The curious *venuli recurrentes* seen in most fossil species but not in Recent ones are not in my opinion a generic difference, since similar *venuli* occur in some, but not in other species of *Angiopteris*.

Marattia anglica (Thomas) n. comb.

Text-fig. 23

1913 *Marattiopsis anglica* Thomas, p. 228, pl. 23, figs. 1-5; text-fig. 1.

EMENDED DIAGNOSIS. Form and size of leaf as a whole unknown. Pinnae borne at right angles to rachis, length over 30 cm. (possibly 50 cm.), base symmetrically contracted, middle region of uniform width, apex usually tapering. Width commonly 15-22 mm., widest 25 mm. Margin entire, midrib up to 3.5 mm. broad, longitudinally grooved. Veins in typical pinna traversing lamina at a concentration of 10-12 per mm. and over most of their course simple, straight and at an angle of 80-85° to the midrib. Free end curving slightly forward, basal end bending back along the midrib and there joining other veins. *Venuli recurrentes* present but inconspicuous.

Hairs absent from lamina, but occurring in small numbers on midrib; straight, simple, 0.5 mm. long.

Fertile pinnae agreeing with sterile in form and venation, synangia typically 4–7 mm. long and occupying about a third of the width of the lamina, composed of up to 30 pairs of sporangia.

Spores oval, mean size $30\mu \times 24\mu$ (range noted 37μ – 26μ long and 33μ – 19μ broad), wall fairly thin, faintly tuberculate, showing one groove.

DISTRIBUTION. *M. anglica* is local but abundant in its four Lower Deltaic localities, Marske Quarry, Hasty Bank, Roseberry Topping and Ryston Nab Quarry (close to Roseberry). It apparently has no associates in these localities with which it is likely to be confused.

DESCRIPTION. The largest pinna fragment seen is still the 30 cm. specimen mentioned by Thomas. The estimated total length of the pinna is based on the taper of the midrib in the larger fragments, but the midrib is difficult to measure accurately and the estimate is at best rough.

About a fifth of the pinna fragments are less than 15 mm. wide, but do not taper like the normal apical regions, and have more crowded veins than usual, up to 18 per cm. Most of these are sterile but Text-fig. 23 shows one with vestigial synangia. Most of these fragments probably represent small more or less sterile leaves. One sterile fragment has a width of 15 mm., but the veins, some of which fork in the lamina, occur at 15 per cm.; this fragment looks like *M. asiatica* but it may be just an abnormal form of *M. anglica*.

Most of the pinna apices seen taper gradually, but there are a few which are rather blunt as described by Thomas (1913).

All the better preserved specimens show dark strands between the veins now recognised by Lundblad (1950: 17) as the same as the fibrous *venuli recurrentes* of *Angiopteris*. No specimen of *M. anglica* shows them as prominent ridges.

Over half the fragments are fertile and though the synangia vary greatly in size they have all opened and shed their spores. Many were macerated and yielded stray spores or none, but in the end one synangium was found that had one loculus still full of spores. The majority of synangia are about 0.8 mm. high and have bent forward or backwards and lie almost on the lamina, the plane of cleavage then passes along them and, missing the lamina, gives the fossil a superficial resemblance to *M. crenulata*. The true margin, however, shows only the slightest bulges at the ends of veins. All the fertile fragments collected by Miss Kendall and by myself were measured. The mean width of all is 17 mm. and of each fertile strip (measured at right angles to the midrib) is 5.6 mm., the synangia themselves being nearly 6 mm. long. Omitting apices and fragments of lamina less than 15 mm. wide the ratios of synangial length to width of lamina are as follows:

Below 24%	2 specimens (18% and 23%)
25–29%	5 specimens
30–34%	8 specimens
35–39%	4 specimens
Above 40%	2 specimens (41% and 44%)

It will be seen that the commonest values lie around 33 per cent.

The only pinna base known is V.13145 previously figured by Thomas (1913, pl. 23, fig. 1.) It has been redrawn under different lighting to show more of the veins (Text-fig. 23 c). The specimen V.12854 (Thomas, 1913, pl. 23, fig. 2) suggests a pinna base (though not described as one). Re-examination of this specimen shows that it is merely a torn and twisted fragment of lamina.

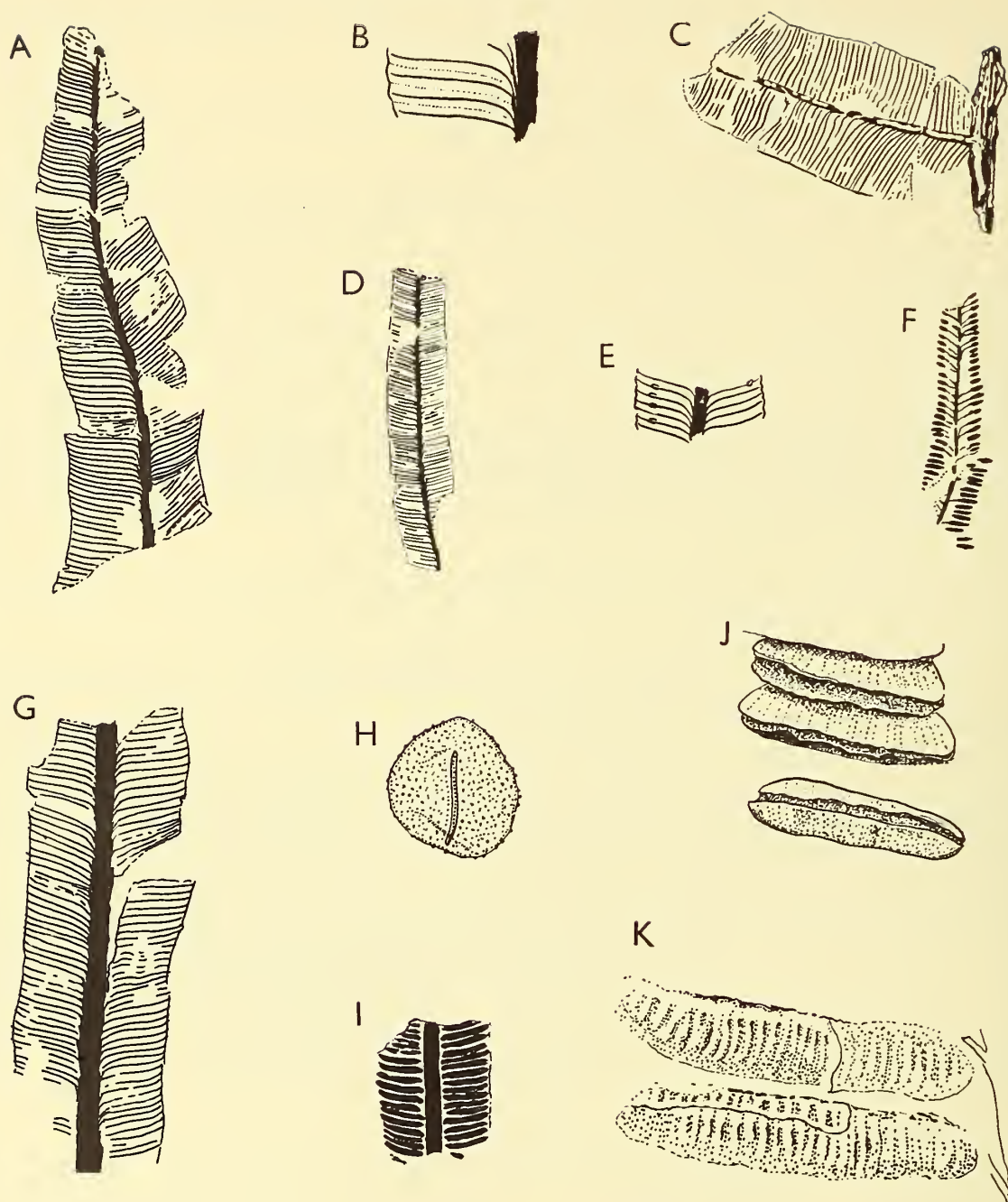


Fig. 23. *Marattia anglica* (Thomas)

A, upper part of sterile pinna, V.31313, $\times 1$. B, veins from A showing the *venuli recurrentes*, $\times 2$. C, base of small sterile pinna, redrawn from original of Thomas (1913, pl. 23, fig. 1), V.13145. D, unusually small sterile pinna, V.31322, $\times 2$. E, small pinna bearing some minute synangia, V.31314, $\times 2$. F, apex of fertile pinna, V.31315, $\times 1$. G, lower part of sterile pinna, V.31316, $\times 1$. H, spore from V.31317, $\times 800$. I, pinna fragment with well developed synangia, V.31318, $\times 1$. J, small synangia, in transfer, V.31319, $\times 12$. K, large synangia as exposed by cleavage, showing internal surfaces of both empty valves, V.31318, $\times 8$.

A, B, are from Ryston Nab Quarry. C, Marske Quarry. D-K, Roseberry Topping.

The rachis in V.13145 shows irregular longitudinal ridges about 0.5 mm. apart. Too little substance remains for hairs to be seen. Although no larger rachis is known fragments of long axes associated with the pinnae at Roseberry Topping may be of this nature. They are about 2 cm. wide and show longitudinal striation rather like *Neocalamites* but irregularly at intervals of 0.5–2.0 mm. The substance is thin and frayed, and, if petioles, they are mere fragments of the fibrous rind. Similar specimens were later noted in all the other localities.

COMPARISON. No other species of *Marattia* occur in Yorkshire. The only rather similar leaves are *Nilssoniopteris vittata* (at once distinguished by its more robust cutinised lamina, as well as by details of the veins) and *Nilssonia tenuinervis* in which the lamina covers the top of the midrib.

Similar Jurassic specimens have been grouped in six species which overlap *M. anglica* but are typically distinct. All agree in the major features of shape, synangia and venation (including the *venuli recurrentes*) except possibly *M. angustifolia*.

The most similar are *M. muensteri* and *M. asiatica*. *M. muensteri* as interpreted by Schenk (1867) and Schimper (1869) has pinnae of similar size and contracted base, but the synangia are only 2–4 mm. long and thus 10–20 per cent of the width of the lamina. European specimens ascribed by various other authors to *M. muensteri* are less perfect and rather more varied (see Harris, 1931: 65) but none specially approaches *M. anglica*.

M. asiatica Kawasaki (1939: 50) is a new name for Zeiller's specimens from Tonkin and for various Japanese and Korean specimens mentioned by Kawasaki and all originally called *M. muensteri*. They mostly show more crowded veins (15–18 per cm.), which may fork in the lamina. The synangia are occasionally as much as 7 mm. long and 28 per cent of the width of the lamina, but mostly rather shorter.

M. hoerensis Schimper (as interpreted by Antevs, 1919 and Harris, 1931) has rather wider pinnae (up to 36 mm.), but with similar veins. The synangia are 2.5–7 mm. long (but typically only 20 per cent of the width of the lamina). The pinna base, which may or may not be expanded, differs in its recurved veins.

M. crenulatus Lundblad (1950) the most different, has wide pinnae (40 mm.), but similar veins. The synangia are very short, barely 10 per cent of the width of the lamina and the margin of both sterile and fertile pinnae is strongly crenulate. Its spores are slightly smaller.

Marattia angustifolia Prinada (1938) has about 13 veins per cm. and synangia apparently up to 25 per cent of the width of the lamina. It seems close to *M. muensteri* but is said to be distinguished by its tapering pinna.

Family OSMUNDACEAE

Genus TODITES Seward, 1900:86

1836 *Acrostichites* Goeppert, p. 284.

EMENDED DIAGNOSIS. Leaf bipinnate, pinnules with a midrib and diverging lateral veins. Fertile pinnules bearing sporangia along the veins on the under side. Sporangia large, ovoid, almost sessile; cells of apical region thickened, opening by a longitudinal slit. Spores with a triradiate scar.

DISCUSSION. *Todites* differs from *Todea* and *Leptopteris* in its sporangia which in the living genera have a much smaller and more lateral patch of thickened cells. Clearly if the

Recent genera are descended from forms like the known Mesozoic fossils, their sporangia have undergone some reduction. An additional reason against using the name *Todea* for the fossils is that there is no good reason for preferring that name to *Leptopteris* for some of the fossils at least. A further reason is that the fossils seem to comprise three groups as different from one another as *Todea* from *Leptopteris*; these might be raised to generic rank but no advantage would be gained by doing so at present. These groups are (1) *Todites princeps* alone; (2) a group of closely similar species centring around *Todites williamsoni* (or else a single polymorphic species); (3) the *Cladotheca* group with several species.

The earlier name *Acrostichites* (Goeppert, 1836) is rejected for reasons given earlier (Harris 1937: 13). The original Latin diagnosis begins by describing the fossil here called *Todites williamsoni*, but it proceeds to describe a *Sagenopteris* and ends by a misinterpretation of the fertile state of *T. williamsoni*. *Acrostichites* is a *nomen confusum*.

The question of the correct name of species with separate sterile and fertile leaves is more difficult. It was suggested (Harris 1937: 14) that where they are quite separate they are organs of different categories and they should have separate names, thus: *Cladophlebis denticulata* and *Todites undans*, but where there is a transition as in *Todites williamsoni* and *T. princeps* the two fossils are scarcely of different categories and one name would serve. A transition being now recognised in *Todites denticulatus* this name is here used for both. The sterile fragment of *T. thomasi* has not been given a distinct name to save tiresome multiplication of names for sterile *Cladophlebis* leaves.

Todites princeps is distinguished by the anadromic order in which its veins and pinnules branch, and this feature is constant. In all other species it is constantly katadromic. Christensen (1920) points out that this character is constant in some fern groups but variable in others. Unfortunately I earlier misunderstood and reversed the terms anadromic and katadromic (Harris 1931: 36) but Text-fig. 50 should make the meaning clear.

Key to the Yorkshire *Todites* species.

- | | | |
|---|----------------------------|---|
| (1) Branching of pinna and of veins anadromic. (Leaf delicate, venation Sphenopterid.) | <i>Todites princeps</i> | |
| Branching of pinna and veins katadromic | | 2 |
| (2) Venation Neuropterid. (Lamina moderately thick, sterile and fertile pinnules similar.) | <i>T. williamsoni</i> | |
| Venation Pecopterid. (Lamina thick, fertile pinnules contracted and with simpler venation.) | Subgenus <i>Cladotheca</i> | 3 |
| (3) Sterile and fertile pinnules attached by a broad base | <i>T. denticulatus</i> | |
| Sterile and fertile pinnules attached by a constricted base | <i>T. thomasi</i> | |

Todites thomasi sp. nov.

Text-fig. 24

DIAGNOSIS. (Size and form of leaves unknown, but for description assumed to be bipinnate. Main rachis unknown.)

In sterile pinna, rachis 1.5 mm. broad, middle region forming a strongly raised band. Pinnules widely spaced, up to 2 cm. long and 4 mm. wide, middle ones arising at an angle of about 80°, rear ones smaller, reflexed. Base of pinnule strongly contracted on both sides. Margins coarsely dentate. Midrib conspicuous, lateral veins arising at intervals of 1 mm. making an angle of about 40° to the midrib, once forked, anterior branch alone running into a tooth. Lamina almost flat, substance rather thick. Hairs absent.

Fertile pinna rachis as in sterile pinna. Pinnules widely spaced, up to 1.2 cm. long and 4 mm. wide. Middle ones arising at right angles to the rachis, rear ones smaller, reflexed. Base of pinnule strongly contracted on both sides. Midrib conspicuous, lateral veins rather obscure above, arising at intervals of about 1 mm. and at an acute angle but probably bending outwards, simple, rather widely spaced. Apex of pinnule blunt, margins entire or showing obscure rounded lobes corresponding to the veins. Margins only slightly recurved, surface of lamina showing more or less strong obliquely placed waves. Substance of lamina dense.

Sporangia attached in large numbers along the fertile veins, oval, showing a strong apical thickened patch of cells. Spores round, with rather thin finely granular walls, mean diameter about 44μ (range noted 40μ – 50μ).

HOLOTYPE. A fertile pinna (Yorkshire Museum).

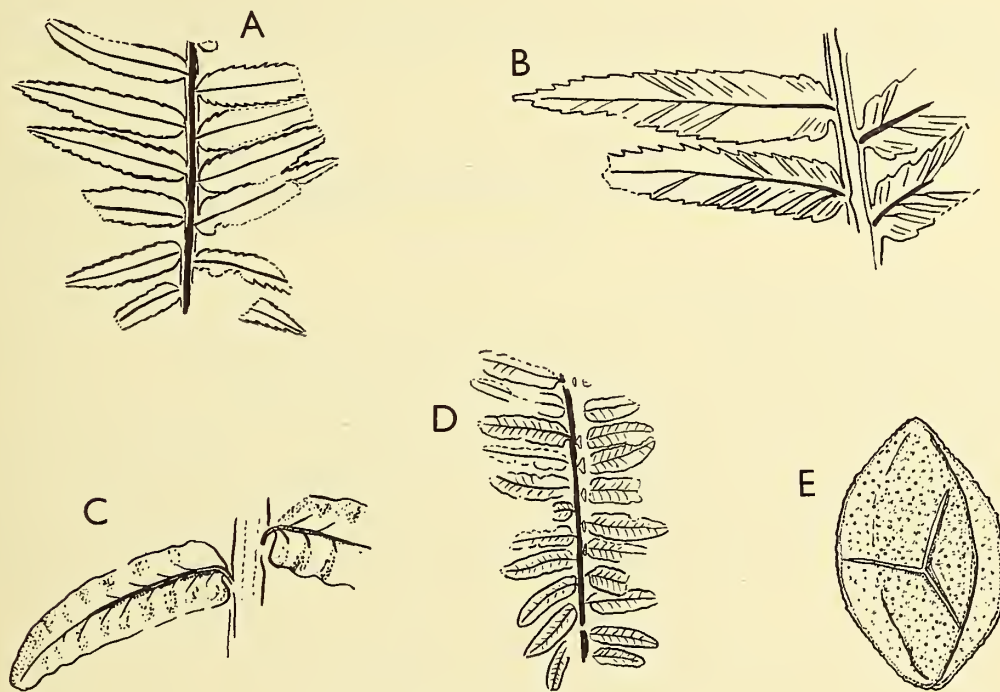


Fig. 24. *Todites thomasi* sp. nov.

A, sterile pinna from the Gristhorpe Bed, V.31475, $\times 1$. B, details of part of A, $\times 2$. C, fertile pinnules, from D, $\times 3$. D, holotype, fertile pinna from Gristhorpe, Yorkshire Museum, $\times 1$. E, spore from D, $\times 800$.

DISTRIBUTION. *Todites thomasi* is only known from the Gristhorpe Bed, Gristhorpe Series, Middle Deltaic.

DESCRIPTION. *T. thomasi* is represented by the two figured specimens only. The holotype, a fertile pinna, bears an old label '*Pecopteris undans*, Upper shale Gristhorpe', and is in a typical Gristhorpe Bed matrix, the other, V.31475, a sterile pinna collected by Dr. Hamshaw Thomas from the Gristhorpe Bed, was recognised by him as new. The two are identified because of the very similar origin of the pinnules, particularly the small, reflexed, lower ones and above all by the very unusual contracted base of the pinnules.

A transfer was made of 1 sq. mm. of one of the fertile pinnules. It revealed plenty of sporangia which were attached to veins in the usual way. On maceration they mostly proved full of spores. The spore masses are somewhat spread out as though the sporangia had burst during preservation and so it was impossible to estimate the volume of the mass, but they give the impression of containing perhaps 200 spores.

T. thomasi is named in honour of Dr. Hamshaw Thomas who collected one specimen, the collector of the holotype being unrecorded.

COMPARISON. The sterile pinna is unlike any *Cladophlebis* known to me; the sterile pinnule of *Kylikopteris arguta* is perhaps least different (in its contracted base). The fertile pinna looks much like '*Cladotheca undans*', i.e. *Todites denticulatus*, in the wavy upper surface of the lamina, but is well distinguished by the pinnules being contracted basally on both sides and by the smaller, reflexed, lower pinnules and by the more oblique veins. None of the other species of the subgenus *Cladotheca* approaches *Todites thomasi* in its fertile pinnules. The spores of *T. thomasi* are possibly a little smaller and more obviously granular than those of *T. denticulatus*.

{ *Todites denticulatus* (Brongniart) Krasser
{ *Cladophlebis denticulata* (Brongniart) Fontaine

Text-figs. 25-27

1. Sterile leaf. Yorkshire specimens.

- 1828 *Pecopteris denticulata* Brongniart, p. 57. (Nomen nudum.)
- 1828 *Pecopteris denticulata* Brongniart, p. 301, pl. 98, figs. 1, 2. (Good leaf, holotype.)
- 1828 *Pecopteris Phillipsi* Brongniart, p. 304, pl. 109, fig. 1. (Lower part of leaf.)
- ?1829 *Pecopteris ligata* Phillips, pl. 8, fig. 14. (Poor sketch.)
- 1833 *Neuropteris ligata* (Phillips): Lindley & Hutton, pl. 69. (Good leaf.)
- 1834 *Pecopteris insignis* Lindley & Hutton, pl. 106. (Large pinnae, figure inaccurate in detail. Leckenby Coll., K.342 Sedgwick Museum, Cambridge.)
- ?1834 *Pecopteris whitbiensis* (Brongn.): Lindley & Hutton, pl. 134. (Figure probably inaccurate in detail.)
- ?1835 *Pecopteris dentata* Lindley & Hutton, pl. 119 in part, larger specimen and pinnule only. (Other specimen is *Todites williamsoni*.)
- 1875 *Pecopteris insignis* L. & H.: Phillips, p. 206, lign. 17. (Sketch of veins and surface pitting.)
- 1875 *Pecopteris denticulata* Brongn.: Phillips, p. 206, lign. 18. (Sketch of veins.)
- ?1875 *Pecopteris dentata* L. & H.: Phillips, p. 208, lign. 21. (Rough sketch.)
- ?1875 *Pecopteris ligata* Phillips: Phillips, p. 206, pl. 8, fig. 14. (As 1829.)
- 1889 *Cladophlebis denticulata* (Brongn.) Fontaine, p. 71. (Name only, specimens probably distinct, see below.)
- 1900 *Cladophlebis denticulata* (Brongn.): Seward, p. 134, pl. 14, figs. 1, 3, 4; pl. 15, figs. 4, 5; pl. 20, figs. 3, 4 (3B is fertile). (Good figures of various parts of leaf.)
- 1900b *Cladophlebis denticulata* (Brongn.): Seward, p. 18, pl. 4, fig. 9. (Good figure of pinna apex.)
- 1910 *Cladophlebis denticulata* (Brongn.): Seward, p. 343, text-fig. 257. (Upper part of sterile leaf), ? text-fig. 256A in part (right hand pinnule), others perhaps *Todites williamsoni*.
- 1911 *Cladophlebis denticulata* (Brongn.): Seward, p. 4, text-fig. 1. (Good sterile leaf; partly as 1900, pl. 14, fig. 3.)
- 1913 *Cladophlebis denticulata* (Brongn.): Thomas, p. 228. (No figure, record from Marske.)
- 1927 *Cladophlebis denticulata* (Brongn.): Hirmer, p. 612, text-fig. 739, 739a (after Seward, 1900).

2. Fertile leaf '*Cladotheca undans*'. Yorkshire specimens.

- 1834 *Pecopteris undans* Williamson in Lindley & Hutton, p. 103, pl. 120. (Fertile pinna. Original in Scarborough Museum, no. 502.39.)
- 1836 *Phlebopteris* ? *undans* (L. & H.): Brongniart, p. 375, pl. 133, fig. 3, 3a, 3b. (Fertile pinna.)
- ?1875 *Phlebopteris undans* (L. & H.): Phillips, p. 203, lign. 12. (Poor figure.)
- 1900 *Cladophlebis denticulata* (Brongn.): Seward, p. 137, pl. 20, figs. 3, 4. (Fertile pinna.)

- 1903 *Cladophlebis denticulata* (Brongn.): Seward & Ford, p. 253, pl. 27, fig. 4. (Rachis and pinna, same figure in 1910.)
- 1910 *Cladophlebis denticulata* (Brongn.): Seward, p. 345, text-fig. 258. (Fertile pinna, good fertile leaf. Original no. K70 Leckenby Coll., Sedgwick Museum, Cambridge.)
- 1911 *Cladotheca undans* (L. & H.): Halle, p. 1, pls. 1, 2. (Pl. 2, figs. 1-5 as Seward, 1910.)
- 1911 *Cladophlebis denticulata* (Brongn.): Thomas, p. 386. (Fertile, brief discussion.)
- 1921 *Cladotheca undans* (L. & H.): Halle, p. 13, pl. 2, figs. 9-12. (Details of sporangia, suggested union with *Todites*.)
- 1921 *Todites denticulatus* (Brongn.): Krasser, p. 355. (Name only.)
- 1923 *Cladotheca undans* (L. & H.): Walton, p. 386, pl. 9, fig. 7; text-fig. 1. (Interpretation of sorus structure.)
- 1931 *Todites denticulatus* (Brongn.): Harris, p. 48, pl. 9, figs. 9, 10. (Sporangia.)
- 1937 *Todites undans* (L. & H.) Harris, p. 14. (Name.)
3. The following fertile specimen from Bornholm is stated by Halle (1921: 14) to be similar to *Cladotheca undans*:
- 1902 *Asplenites cladophleboides* Müller, p. 27, pl. 2, fig. 20.
4. Sterile specimens from other regions which have been identified as *Cladophlebis denticulata* or with its synonyms and need further study for reliable determination or else, as noted below, are distinct.
- 1868 *Alethopteris insignis* Eichwald, p. 15, pl. 11, fig. 6. (Russia.)
- 1889 *Cladophlebis denticulata* (Brongn.): Fontaine, p. 71, pl. 7, fig. 7, pl. 4, fig. 2. (Small fragments with rather different veins. American Cretaceous.)
- 1894 *Cladophlebis denticulata* (Brongn.): Raciborski, p. 224, pl. 22, figs. 3, 4. (More coarsely dentate than in Yorkshire. Poland.)
- 1894 *Cladophlebis insignis* (Eichwald): Raciborski, p. 81, pl. 22, figs. 9, 10. (Pinnules entire. Poland.)
- 1905 *Cladophlebis denticulata* (Brongn.): Fontaine in Ward, p. 68, pl. 11, figs. 1-7. (Small fragments. American Cretaceous.)
- 1907 *Cladophlebis denticulata* (Brongn.): Seward, pp. 5, 21, pl. 1, figs. 8, 9 (pinnules with entire margin), pl. 2, fig. 33 (pinnules with different venation), pl. 3, fig. B (margin entire ?), pl. 4, figs. K-N (margin entire). (Caucasia and Turkestan.)
- 1910 *Cladophlebis denticulata* (Brongn.): Kryštofovich, p. 5, pl. 1, fig. 1, 1a (veins different). (Ussuriland.)
- 1911 *Cladophlebis denticulata* (Brongn.): Thomas, pp. 14, 63, pl. 2, figs. 10-12. (Venation different ?. Kamenka, Russia.)
- 1911 *Cladophlebis denticulata punctata* Thomas, pp. 15, 65, pl. 2, fig. 13, 13a. (Distinguished by punctate rachis. Kamenka, Russia.)
- 1911a *Cladophlebis denticulata* (Brongn.): Seward, p. 668, pl. 2, figs. 31-36, 38; pl. 6, figs. 8, 9 (not pl. 8, fig. 29). (Fragments. Upper Jurassic; Scotland.)
- 1912 *Cladophlebis denticulata* (Brongn.): Seward, p. 16, pl. 2, figs. 30, 30a, 36; pl. 3, figs. 37, 37a, 38. (Fragments with similar pinnules. Afghanistan.)
- 1913 *Cladophlebis denticulata* (Brongn.): Halle, p. 12, pl. 2, figs. 7-9. (Specimens from Graham Land renamed *C. grahami* by Frenguelli, 1947.)
- 1914 *Cladophlebis* cf. *denticulata* (Brongn.): Gothan, p. 22, pl. 18, fig. 5. (Fragment, more like *Todites hartzi* Harris. Germany.)
- 1916 *Cladophlebis denticulata* (Brongn.): Kryštofovich, p. 105, pl. 9, figs. 3-6. (Perhaps identical but fine details obscure. Ussuriland.)
- 1917 *Cladophlebis denticulata* (Brongn.): Arber, p. 31, pl. 4, fig. 6. (Good pinnule. New Zealand.)
- 1925 *Cladophlebis denticulata* (Brongn.): Kawasaki, p. 11, pl. 9, fig. 34; pl. 10, figs. 35-38; pl. 36, fig. 100; pl. 40, figs. 108, 109; pl. 46, fig. 123. (Korea.)
- 1926 *Cladophlebis denticulata* (Brongn.): Kawasaki, p. 2, pl. 1, fig. 1. (Margins scarcely dentate. Korea. Kawasaki, 1939, renames these specimens *Cladophlebis Kogendoensis*.)
- 1926 *Cladophlebis* cf. *denticulata* (Brongn.): Kryštofovich, p. 600, pl. 12, fig. 1. (Pinnulae, no details. Caucasus.)
- 1927 *Cladophlebis denticulata* (Brongn.): Kryštofovich, p. 560, pl. 31, figs. 1, 2. (Very small pieces. Central Siberia.)
- 1928 *Cladophlebis denticulata* (Brongn.): Makarewiczówna, p. 13. (No figure. Lower Lias; Poland.)
- 1928 *Cladophlebis denticulata* (Brongn.) Yabe & Oishi, p. 5, pl. 1, figs. 3, 4. (Fragment, margins entire. Japan.)

- 1930 *Cladophlebis denticulata* (Brongn.): Turutanova-Ketova, p. 134. (No figure. Central Asia.)
- 1930a *Cladophlebis denticulata* (Brongn.): Turutanova-Ketova, p. 320. (No figure. Central Asia.)
- 1931b *Cladophlebis denticulata* (Brongn.): Oishi, p. 233, pl. 1, fig. 5, 5a. (Fragment, margin entire. Japan.)
- 1931 *Cladophlebis denticulata* (Brongn.): Sze, pp. 2, 30, pl. 1, fig. 1; pl. 4, fig. 4. (Possibly identical, but details, obscure. China.)
- 1931 *Cladophlebis* cf. *denticulata* (Brongn.): Prinada, p. 17, pl. 1, fig. 8. (Small fragment. Central Asia.)
- 1932 *Cladophlebis denticulata* (Brongn.): Oishi, p. 283, pl. 11, figs. 3-7. (Fragments, margins entire ?. Japan.)
- 1933a *Cladophlebis* cf. *denticulata* (Brongn.): Sze, p. 10, pl. 6, figs. 5-7. (Fragments. China.)
- 1933 *Cladophlebis denticulata* (Brongn.): Prinada, p. 30, pl. 1, fig. 7; pl. 3, fig. 13. (Margins of pinnules entire ?. Transcaucasia.)
- 1933 *Cladophlebis denticulata* (Brongn.): Kryshstofovich, pl. 10, fig. 2. (Upper part of leaf, same figure as Seward, 1907, pl. 4, fig. N. Angaraland.)
- 1933 *Cladophlebis denticulata* var. *punctata* Thomas: Yabe & Oishi, p. 207, pl. 31, figs. 1, 2. (Distinguished by punctate rachis.)
- 1933 *Cladophlebis denticulata* (Brongn.): Yabe & Oishi, p. 206, pl. 30, fig. 8. (Small fragment. Manchuria.)
- 1935 *Cladophlebis denticulata* (Brongn.) and *C. denticulata* v. *punctata* Thomas: Brick, pp. 12, 15, pl. 1, figs. 1, 2, 4, 5; text-figs. 3, 4. (Fragments, rachis punctate ?. Ferghana.)
- 1936 *Cladophlebis* cf. *denticulata* (Brongn.): Turutanova-Ketova, p. 92, pl. 1, fig. 4. (Small fragment. Central Asia.)
- 1936 *Cladophlebis denticulata* (Brongn.): Oishi & Takahasi, p. 118, pl. 1, fig. 2. (Japan.)
- 1940 *Cladophlebis denticulata* (Brongn.): Oishi, p. 256, pl. 48, fig. 1. (Pinnules rather smaller than usual. Japan.)
- 1940 *Cladophlebis denticulata* (Brongn.): Sitholey, p. 6, pl. 1, figs. 9-14; pl. 2, figs. 17, 18; pl. 7, figs. 87-89. (Fragments, possibly identical. Afghanistan.)
- 1947 *Cladophlebis denticulata* (Brongn.): Frenguelli, p. 17. (Exclus. fig. et synonym. partim.) Discussion.
- 1949 *Cladophlebis denticulata* (Brongn.): Takahasi, p. 135, text-figs. 1-4. (Redescribed, Takahasi, 1950, p. 439 as *Todites recurvatus* Harris. Sterile and fertile fragments. Japan.)
- 1949 *Cladophlebis denticulatus* (Brongn.): Sze, p. 4, pl. 13, figs. 11, 12; pl. 14, figs. 1, 2. (Good specimens, fine details not shown. Hupeh, China.)
- 1951 *Cladophlebis denticulata* (Brongn.): Menéndez, p. 173, pl. 4, figs. 1-4. (Small fragments, margins entire ?. Argentine.)
- 1952 *Cladophlebis denticulata* (Brongn.): Sze & Lee, pp. 4, 23, pl. 6, fig. 2; pl. 7, figs. 5, 6. (Small fragment.) Szechuan, China.)
- 1956 *Cladophlebis denticulata* (Brongn.): Semaka, p. 111, text-figs. 4, 17-19. (No teeth, pinnule base contracted. Lias; Roumania.)
- 1957 *Cladophlebis denticulata* (Brongn.): Stanislavski, p. 43, pl. 4, figs. 2, 3; text-fig. 15. (Fragments. S. Russia.)

The specimens listed by Seward (1900) under the following names are believed to be distinct: *Cladophlebis australis* (McCoy), *Cladophlebis indica* (Oldham & Morris), *Cladophlebis* cf. *nebbensis* Raciborski, *Cladophlebis Roesserti Groenlandica* Hartz, *Cladophlebis stewartiana* Hartz, *Asplenium petruschinense* Heer, *Pteris frigida* Heer, *Pteris longipennis* Heer.

Although this list of comparable forms is considerable it is doubtless incomplete. At least as long a list of equally similar ferns described under other specific names could be given.

EMENDED DIAGNOSIS. Sterile and fertile leaves separate although probably of similar size and shape but pinnules dimorphic. Lamina as a whole lanceolate, estimated typical dimensions, 1 m. \times 40 cm. but base and petiole not known.

Rachis up to 7 mm. wide, rounded below, but with a flat-topped ridge on the upper side. Pinnae arising at intervals of about 4 cm. and at an angle of 60°-75° in lower part of leaf but at shorter intervals and an angle of about 40° above. Pinna rachis rounded below but with a ridge above, first pinnule arising on basiscopic side (katadromic), origin close to main rachis.

Typical sterile pinnules in lower and middle parts of leaf 2.5-3.0 cm. long, rarely longer, 5-6 mm. wide in the middle, 6-7 mm. wide basally; apex rather abruptly narrowed; pinnule arising at an angle of 60°-70° to the pinna rachis and nearly straight. In upper parts of leaf, pinnules smaller and relatively shorter, pointing more forwards. Towards ends of pinnae,

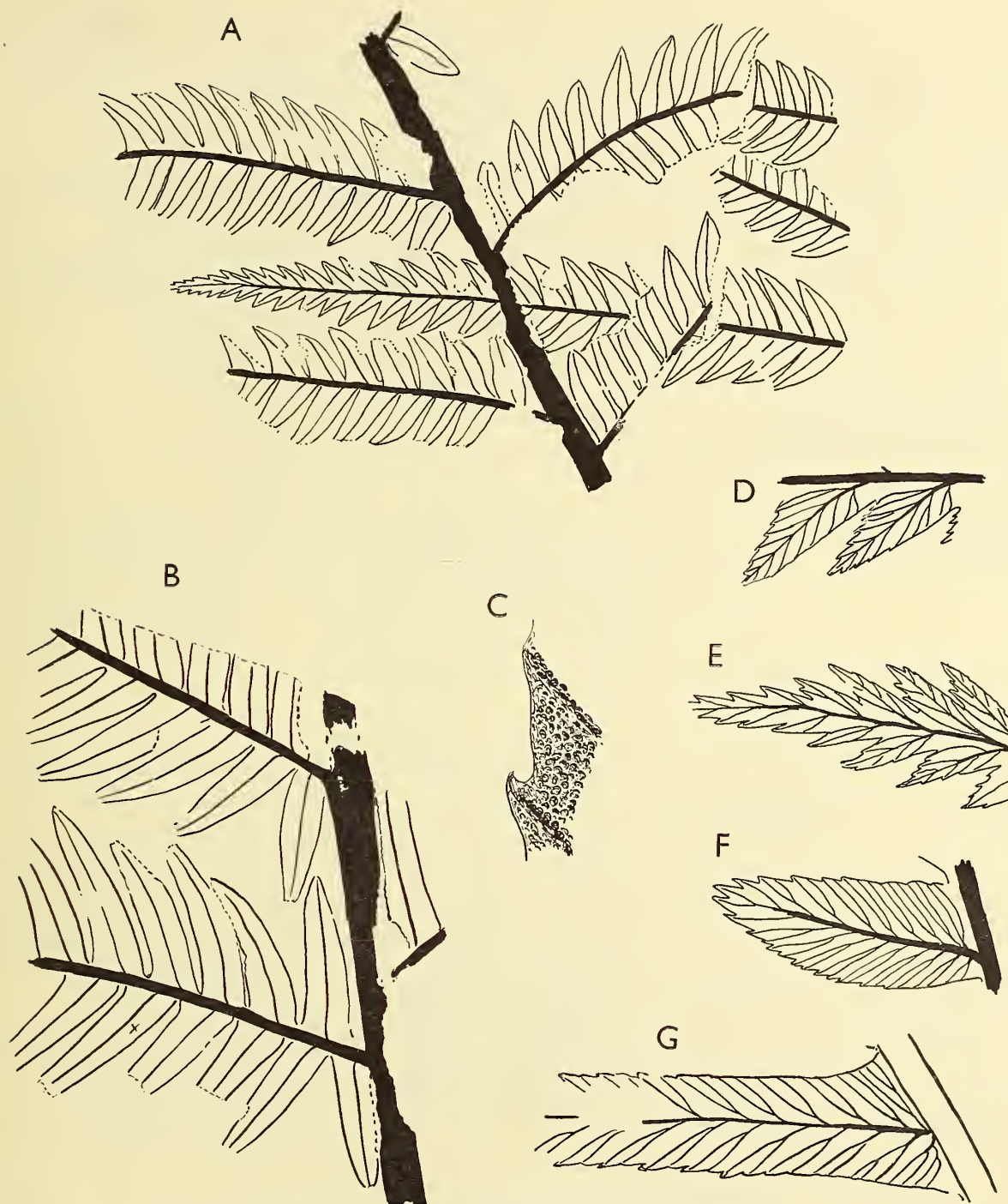


Fig. 25. *Todites denticulatus* (Brongniart), sterile leaf
[*Cladophlebis denticulata* (Brongniart)]

A, middle region of one leaf and almost complete pinna from about 15 cm. from the top of another leaf. Only about half the specimen is shown. Leckenby Coll. K60, Sedgwick Museum, Cambridge, $\times 1$. B, lower part of a leaf. J.5009, Oxford Museum of Geology. Nearly half omitted, $\times 1$. C, margin of a pinnule of B, showing the teeth and surface markings (rough sketch only), $\times 30$. D, E, portions from near the apex of the separate pinna of A, $\times 3$. F, pinna marked X in A, $\times 3$. G, pinna marked X in B, $\times 3$.

A, localised as Scarborough, but in Gristhorpe Bed matrix. B, Whitby.

pinnules curving forwards (falcate), contracting steadily from the base to the acute apex. Basal pinnules on basiscopic side somewhat specialised; in lower part of leaf tending to arise at a large angle and to lie over the main rachis, in middle part of leaf length tending to be less than that of the second pinnule, in upper part of leaf length often much reduced.

Margins of pinnules always dentate, at least in upper parts, but occasionally recurved and concealing the teeth. Teeth often alternately large and small, sharp, forward pointing. Pinnule base expanded on acroscopic side, scarcely expanded or contracted at basicopic side. Substance of lamina thick, upper surface covered with cellular pits 30μ wide. Midrib of pinnule giving off its first branch on the basiscopic side (katadromic); basal pair of veins forked twice, other veins forked once, branch veins almost straight, reaching the margin at a concentration of 12–15 per cm. and at an angle of about 50° , but more crowded in small pinnules.

Typical fertile pinnules 15 mm. \times 3–4 mm. but often smaller, arising at 75° – 80° to the rachis and rather widely spaced, margins dentate with large rounded teeth, but teeth smaller or hardly developed in small pinnules. Apex of pinnule blunt, base slightly expanded on acroscopic side but contracted on basiscopic side. Substance of lamina fairly thick, often irregularly wrinkled, upper surface often transversely waved, margins slightly depressed. Midrib conspicuous but lateral veins inconspicuous, simple, about 8 per cm. On under side sporangia thickly covering veins, persistent. Sporangia ovoid-cylindrical about $400\mu \times 250\mu$ with a short broad stalk and a large apical area of thickened cells. Spore mass nearly cylindrical. Spores round, mean diameter about 37μ (range noted 25μ – 48μ) with a thin minutely punctate (almost smooth) wall. Triradiate cracks fine, nearly as long as the spore radius, without thickened margins.

DISTRIBUTION. *Todites denticulatus* occurs throughout the Deltaic Series but is only abundant at two localities and even there it is local. These are the Whitby Plant Bed (Lower Deltaic) and the Gristhorpe Plant Bed (Middle Deltaic). The fertile fragments are known from these localities only. Elsewhere the species is represented by scattered sterile fragments. As indicated in the synonymy leaves identified with it have been reported from Jurassic and Cretaceous floras from many regions but these cannot yet be accepted.

DISCUSSION. This species is included in *Todites* because it is regarded as correct to extract species from form-genera such as *Cladophlebis*. Where, however, one is dealing with sterile material only the name *Cladophlebis denticulata* is considered correct.

I believe that this fine leaf is of fairly constant form; the numerous magnificent slabs of sterile leaves in Museums show a perfect transition from the basal parts with large pinnules (*insignis* form) to upper parts with small triangular pinnules. The figures of Brongniart and of Seward show the general aspect of the leaf very well, though not of course representing all the finer details; the figures of Lindley & Hutton are less accurate, while those of Phillips are diagrammatic sketches. All the specimens figured by Seward show marginal teeth on examination as does specimen no. K342 in the Sedgwick Museum, the original of *Pecopteris insignis* Lindley & Hutton (1834, pl. 106).

The ridge on the upper side of the rachis of both sterile and fertile leaves is sometimes a conspicuous feature, but often modified by collapse in compression. Very few sterile pinnules exceed 3.0 cm. long, and Seward's figure of up to 4 cm. perhaps refers to the specimen described and figured as *Pecopteris insignis* by Lindley & Hutton (1834, pl. 106). All well preserved sterile pinnae show a pitted surface, a feature which Phillips seems to have noticed.

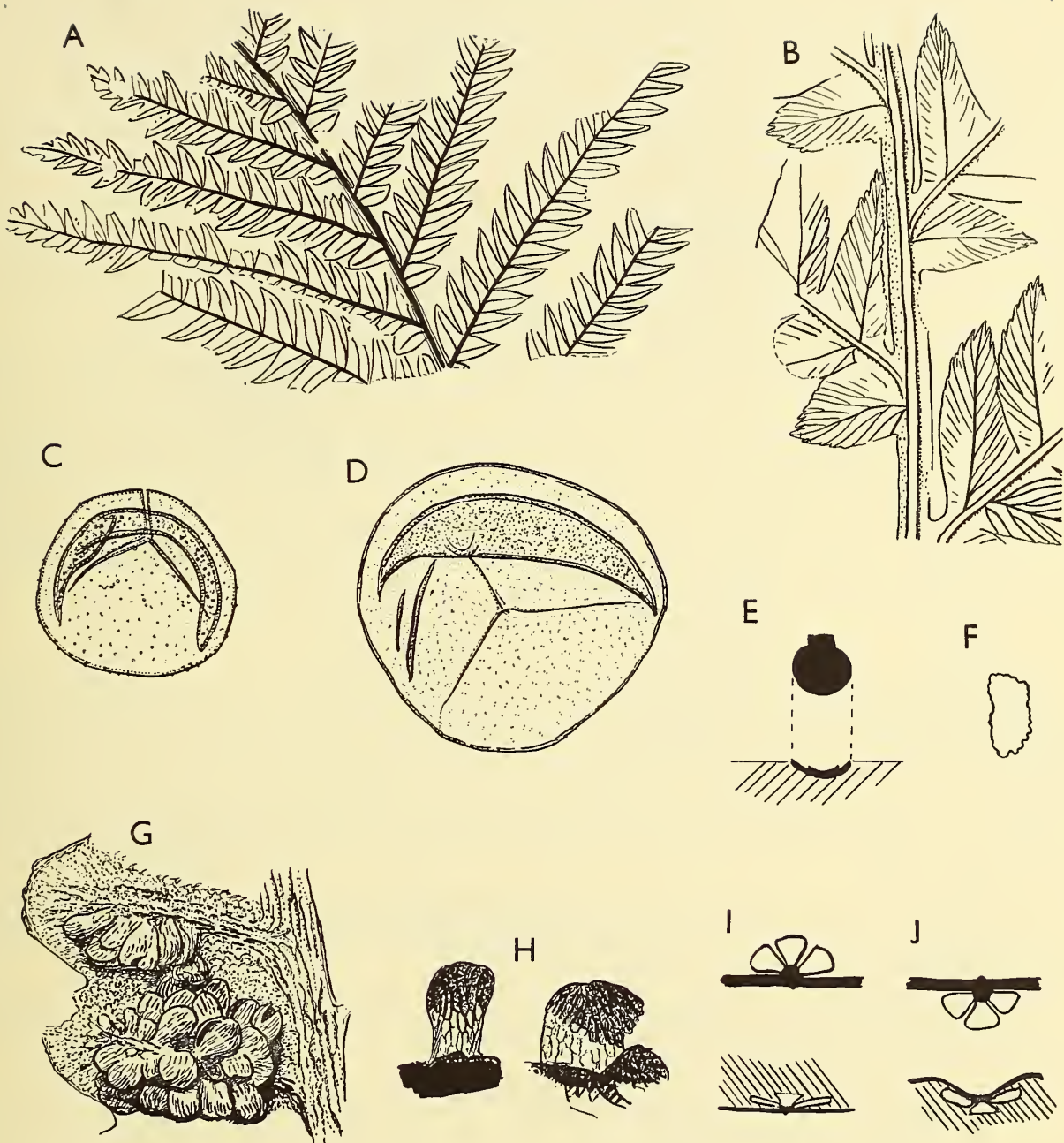


Fig. 26. *Todites denticulatus* (Brongniart), sterile (= *Cladophlebis denticulata*) and fertile (= *Cladotheca undans*).

A, upper part of sterile leaf, V.31471, $\times 1$. B, part of A, $\times 3$. C, D, spores from one leaf, V.25868, $\times 800$. E, diagram to suggest the form of the compressed rachis in the rock matrix (below) and its original form. F, intact spore mass, V.25868, $\times 40$. G, details of Walton's original transfer showing one nearly intact sporangial mass and another with most sporangia rubbed off. V.31474, $\times 20$. H, two empty sporangia by transmitted light to show the thick cells at the apex, V.25868, $\times 40$. I, J, diagrams to relate the form of the fertile lamina to its original position. I, inverted and therefore flat. J, with sporangia downwards and lamina collapsing onto them.

All from the Gristhorpe Bed.

Fertile leaves are rarer than the sterile and not merely less conspicuous; of this I am sure from my own collecting. Such fertile specimens as show the main rachis indicate that the fertile leaf is fully fertile. The plane of cleavage nearly always passes over the upper surface of the fertile pinnule, but the lamina can be picked away to expose a few sporangia (Halle, 1911: 1921) and readily gives excellent transfers exposing all of them (Walton 1923), these transfers prove that the fertile vein is thickly covered with sporangia. Halle showed that the sporangia have a large apical thickened area and are not the same as in *Todea*. All the sporangia clearly seen had dehisced and on maceration gave only scattered spores but in the end a compact mass was found representing an unopened sporangium. This mass, which is a flattened cylinder, did not appear suitable to macerate further in order to isolate the spores for a count, but from its estimated volume it may consist of about 150 closely packed spores.

In about half the fertile specimens the upper surface is strongly marked by transverse waves, the veins being near the bottoms of the hollows. The others show a nearly flat surface with veins standing up as slight ridges. The difference is accountable on the basis of Walton's (1936) theory of compression (see Text-fig. 26 I, J). Where the leaf is preserved with sporangia facing upwards, little deformation would be expected apart from a general flattening. On the other hand where the sporangia face downwards they would displace rock matrix and finally the lamina would collapse into the hollow provided by the sporangia. In both cases cleavage occurs on the upper side. This hypothesis still needs to be tested in the field.

Recognition of sterile and fertile leaf as the same species.

Although *Cladophlebis denticulata* and *Pecopteris undans* agree in size and branching, their pinnules are quite different and the credit for recognising their identity must be given to Nathorst. All subsequent authors who have studied the species in the field or laboratory (Seward 1900: 139; Thomas 1911a; Halle 1911, 1921; Harris 1931) have accepted it but the evidence was never published and since Frenguelli (1947) has denied their identity it is here stated rather fully.

(1) Striking association of the fertile fragments with sterile leaves in particular parts of the Gristhorpe Bed and the Whitby Plant Bed, the two best localities for the sterile leaf. The fertile leaf is known from nowhere else.

(2) Essential similarity of the two leaves in size and shape of the main and branch rachises and in the rib on the upper surface of the smaller rachises and in the manner of origin of the pinnules.

(3) The final evidence of continuity was recently provided by a specimen collected by Mr. F. M. Wonnacott, which shows sterile pinnules on one side, half sterile, half fertile ones on the other. The sterile parts though rather narrow have normal teeth, veins and surface pitting. The fertile parts have their normal margin, veins and surface below but near the transition the veins fork. Such specimens must be rare as it is the only one of its kind seen.

COMPARISON. (1) *Yorkshire material*. The only similar sterile leaves are *Todites thomasi* (q.v.), *Cladophlebis haiburnensis* (q.v.) and *Todites williamsoni* with which small pinnules from the upper part of the leaf have sometimes been confused. They are, however, sharply distinguishable. In *T. williamsoni* the margin is scarcely ever denticulate, while in *T. denticulatus* it is always denticulate even if the teeth may be small and hard to see. In *T. williamsoni* the basal veins are usually branched more than twice, while in *T. denticulatus* the veins are all branched

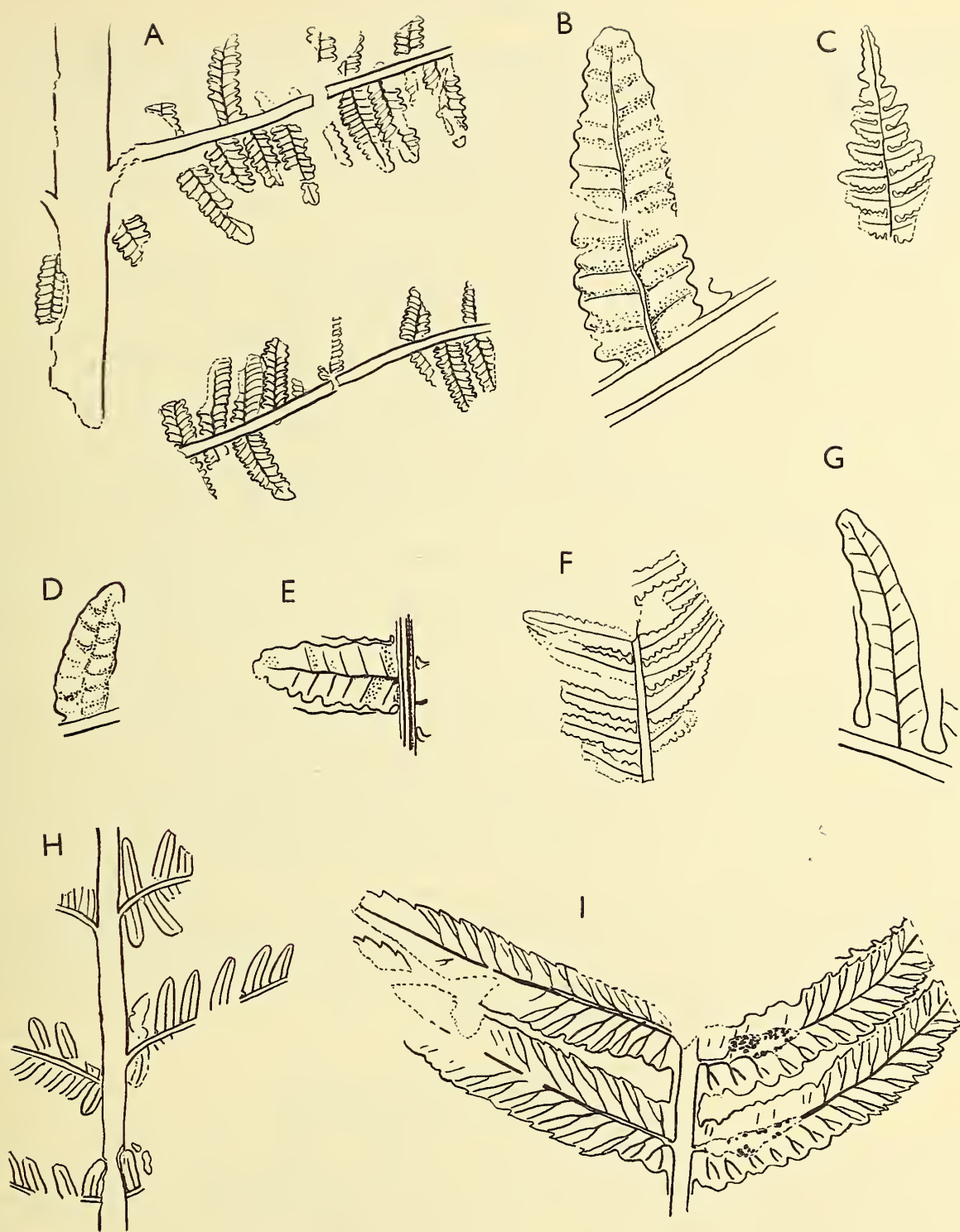


Fig. 27. *Todites denticulatus* (Brongniart), fertile (= *Cladotheca undans*)

A, lower part of fertile leaf (half omitted), 39245, $\times 1$. B, pinnule from upper part of 39245, not included in A, $\times 3$. C, apex of fertile pinna (see also E), V.25881, $\times 2$. D, pinnule from H, $\times 3$. E, pinnule from C, $\times 3$. F, partly sterile specimen (see I). The pinnules on the left are almost completely sterile, those on the right partly fertile, V.28491, $\times 1$. G, elongated form of pinnule, V.28492, $\times 3$. H, middle region of leaf, V.31473, $\times 1$. (Not all shown.) I, details of F, some of the lamina has been picked away to show sporangia, $\times 3$.

A, B, imperfectly localised but appears to be from Gristhorpe. C, E-G, I, Gristhorpe Bed. D, H, Whitby Plant Bed.

once, apart from the basal pair and the uppermost. It is because there is so little chance of confusion that I have ventured to identify certain poorly figured Yorkshire specimens.

(2) *Material outside Yorkshire*. Here comparison and determination are most difficult because the possibilities are nearly endless. A sterile *Cladophlebis* of this group is only determinable with specimens large enough to show the general form and fine enough to show venation and teeth and even then difficult. The references to this species have therefore not been placed in categories, but merely cited with a brief comment.

Partial comparison is possible between *T. denticulatus* and *T. thomasi*, p. 76 and full comparison with a few species of the Greenland Rhaeto-Liassic where both sterile and fertile leaves are known. The most similar of these is *T. scoresbyensis* (Harris 1931) where the sterile leaf is very similar indeed. A small difference in *T. scoresbyensis* is that in the lower part of the leaf the first basiscopic pinnule does not tend to lie over the rachis, and in the upper part the first pinnule is less rounded in shape. The fertile leaf differs considerably in its incurved pinnule margin. Two other species, *T. hartzi* and *T. recurvatus* differ more considerably in their relatively shorter sterile pinnules and in their less lobed fertile ones. The only hope for clearing up the confusion over *Cladophlebis* species lies in the use of additional diagnostic characters and the fertile leaves provide several. It may be that fertile leaves are by no means as rare as the literature suggests but that they are missed in collecting because they make unattractive specimens. There are in fact figures of several *Cladophlebis*-like pinnules in the older literature, e.g. 'Asplenites' with *Cladophlebis nebbensis* in Sweden (Nathorst 1876); *Cladophlebis szeiana* in part (P'an 1936, pl. 7, figs. 5, 7); *Cladophlebis palibinii* Prinada (1938); *Cladophlebis argutula* in part, Kawasaki (1936, pl. 4, fig. 14). There are also specimens recognised as fertile *Cladophlebis* sp. (Carpentier & Lamare 1932, pl. 8, figs. 3, 4); *Osmundites prigorovskii* (Kryshtofovich & Prinada 1933, especially pl. 1, fig. 4), and *Todites recurvatus* Takahasi (1950, text-figs. 3-5). The fact that the sporangia are always embedded in the rock is now an advantage for a balsam transfer exposes them more perfectly than the plane of cleavage could ever do.

The name '*denticulata*' became very much used about thirty years ago, both for good material and for tiny fragments not always showing fine details. Later there was a tendency to remove and redescribe the better material under new names leaving a pile of near rubbish as '*denticulata*' (the specific name *nebbensis* has suffered in the same way). Clearly a better name for a fragment would be *Cladophlebis* cf. *denticulata*.

Abnormal leaves doubtfully identified as

***Cladophlebis denticulata* (Brongn.)**

Two specimens were noted in old collections which stand in isolation from the main bulk of material. Both are sterile and probably from the Gristhorpe Bed.

(1) In the Yorkshire Museum a leaf with pinnules for the most part irregularly contracted but at occasional points expanded and even partly branched. A few pinnules show the normal *denticulata* form in places. It is regarded as a pathological form resulting from injury to a frond in early development.

(2) The Sedgwick Museum specimen no. K.58. This is a fragment from the middle region of a regularly grown leaf. Its unusual feature is that the pinnules are very small (9 mm. × 2.5 mm.) and the margins entire. The basal veins are twice forked and all the rest are once

forked, as in a normal pinnule of *denticulata*, but much more crowded, reaching the margin at a concentration of about 40 per cm. In texture it resembles *denticulata*. The specimen bears the labels *Cladophlebis denticulata*, *Pecopteris whitbiensis* and, in Nathorst's writing 'Pecopteris whitbiensis variety allied to *asplen. argutulum* Heer A.N.'

It may be a rare abnormal form of *denticulata*, but it might also be the only specimen in Yorkshire of some other species. A single specimen of a *Cladophlebis* species is not in general worth description.

Todites williamsoni (Brongn.) Seward

Text-figs. 28, 29

1. Yorkshire specimens.

- 1828a *Pecopteris Williamsoni* Brongniart, p. 57. (Name only.)
- 1829 *Pecopteris recentior* Phillips, pl. 8, fig. 15. (Sterile fragment.)
- 1829 *Pecopteris curtata* Phillips, p. 148, pl. 8, fig. 12. (Fertile fragment.)
- 1829 *Pecopteris hastata* Phillips, p. 148, pl. 8, fig. 17. (Fragment of sterile pinna apex.)
- 1829 *Pecopteris Williamsoni* Brongn.: Phillips, pl. 10, fig. 7. (Sterile fragment.)
- 1833 *Neuropteris recentior* (Phillips) Lindley & Hutton, p. 195, pl. 68. (Sterile leaf.)
- 1834 *Pecopteris Williamsoni* Brongn.: Brongniart, p. 324, pl. 110, figs. 1, 2. (Good fertile leaf.)
- 1834 *Pecopteris Whitbiensis* Brongniart, p. 321, pl. 109, figs. 2-4. (Good sterile leaf.)
- 1834 *Pecopteris tenuis* Brongniart, p. 322, pl. 110, figs. 3, 4. (Sterile leaf.)
- 1834 *Pecopteris Williamsoni* Brongn.: Lindley & Hutton, p. 125, pl. 126. (Fertile pinnae.)
- 1835 *Pecopteris dentata* Lindley & Hutton, p. 55, pl. 169 in part. (Leaf apex and small pinnules only, others—*T. denticulatus*.)
- 1836 *Acrostichites williamsoni* (Brongn.) Goeppert, p. 285, in part. (Name.)
- 1875 *Pecopteris Whitbiensis* Brongn.: Phillips, p. 208, pl. 8, fig. 17. (*P. hastata* of Phillips, 1829.)
- 1875 *Pecopteris Williamsoni* Brongn.: Phillips, p. 209, pl. 10, fig. 7 (as 1829); lign. 23. (Fertile fragment.)
- 1875 *Pecopteris curtata* Phillips: Phillips, p. 209, pl. 8, fig. 12 (as 1829).
- 1875 *Pecopteris recentior* Phillips: Phillips, p. 211, pl. 8, fig. 15 (as 1829).
- 1900 *Todites williamsoni* (Brongn.) Seward, p. 87, pl. 14, figs. 2, 5, 7; pl. 15, figs. 1-3; pl. 21, fig. 6; text-fig. 12. (Good sterile leaves and fertile pinnules; synonyms; discussion.)
- 1900b *Todites Williamsoni* (Brongn.): Seward, p. 8, pl. 1, fig. 1 (Lindley & Hutton, 1835, pl. 169 refigured), pl. 1, fig. 2. (Sterile leaf.)
- 1903 *Todites williamsoni* (Brongn.): Seward & Ford, p. 252, pl. 27, figs. 1, 8, 9, 11, 13. (Good fertile leaves, sporangia.)
- 1908 *Todites williamsoni* (Brongn.): Nathorst, p. 7, pl. 1, fig. 7. (Spore mass.)
- 1911a *Todites williamsoni* (Brongn.): Thomas, p. 386, pl. 3, figs. 8, 9. (Sporangia and spores.)

See Seward (1900: 87) for citations of *Todites williamsoni* in the literature.

2. Specimens from other regions resembling *Todites williamsoni* (including the Rhaetic *Todites goeppertianus* but excluding Keuper records).

- 1846 *Neuropteris Goeppertiana* Münster in Goeppert, p. 104, pl. 8, 9, figs. 9, 10. (Sterile leaf.)
- 1867 *Acrostichites Goeppertianus* (Münster) Schenk, p. 44, pl. 5, fig. 5; pl. 7, fig. 2. (Sterile and fertile pinnules. Rhaeto-Liassic of Franconia.)
- 1868 *Acrostichites Williamsoni* (Brongn.): Eichwald, p. 17, pl. 2, fig. 3. (Jurassic; Russia.)
- 1878b *Acrostichites Goeppertianus* (Münster): Nathorst, p. 43, pl. 5, figs. 7, 8a. (Fertile fragments. Lower Lias; Sweden.)
- 1885 *Todea williamsoni* (Brongn.) Schenk, p. 168, pl. 3, fig. 3, 3a, b. (Fertile fragment, schematic drawings of sporangia and spores. China.)
- 1889 *Asplenium whitbiense* (Brongn.) Yokoyama, p. 31, pl. 3, fig. 3; pl. 10, figs. 1, 2a. (Sterile. Japan.)
- 1892 *Todea williamsoni* (Brongn.): Raciborski, p. 1, pl. 2, fig. 15. (Details of sporangia, similar figs. in 1894.)
- 1894 *Todea williamsoni* (Brongn.): Raciborski, p. 158, pl. 6, figs. 17-20. (Good fertile pinnules. Poland.)
- 1894 *Cladophlebis whitbiensis* (Brongn.) Raciborski, p. 215, pl. 21, figs. 1, 2, 8-10. (Good sterile pinnae. Poland.)

- 1894 *Cladophlebis solida* Raciborski, p. 221, pl. 24, figs. 10–13. (Good sterile leaves. Poland.)
 1896 *Todea williamsoni* (Brongn.): Hartz, p. 232, pl. 12, fig. 4, 4a. (Fertile. Lias; Greenland.)
 1903 *Cladophlebis (Todea) Roesserti* Zeiller, p. 38, pl. 2, figs. 1–7; pl. 3, figs. 1–3. (Good sterile and fertile leaves, sporangia. Tonkin. Frenguelli (1947) distinguishes the sterile leaves of this and some others as *Cladophlebis gondwanensis* Frenguelli.)
 1911a *Todites williamsoni* (Brongn.): Seward, p. 667, pl. 2, fig. 27, 27a; pl. 4, fig. 57; pl. 7, fig. 15. (Sterile leaves. Upper Jurassic; Scotland.)
 1912 *Todites williamsoni* (Brongn.): Kryshfovich, p. 491, pl. 15, figs. 2, 3. (Sterile fragments. E. Urals.)
 1913 *Todites williamsoni* (Brongn.): Halle, p. 11, pl. 3, figs. 1–5; pl. 8, fig. 1b. (Antarctica.)
 1915 *Todites williamsoni* (Brongn.): Kryshfovich, p. 96, pl. 3, fig. 3. (Fragment. Amurland.)
 1919 *Todites williamsoni* (Brongn.): Antevs, p. 20, pl. 1, figs. 20–22. (Ill preserved. Lower Lias; Sweden.)
 1926 *Todites cf. williamsoni* (Brongn.): Harris, p. 55, text-fig. 2 F. (Sterile fragment. Rhaetic; Greenland.)
 1928 *Todites williamsoni* (Brongn.): Walkom, p. 459, pl. 26, figs. 1, 2. (Sterile and fertile pinnae. Queensland.)
 1931 *Cladophlebis (Todites) whitbiensis* (Brongn.): Sze, pp. 47, 52, pl. 10, figs. 1, 2. (Sterile pinnae. China.)
 1931 *Todites goeppertianus* (Münster): Harris, p. 31, pl. 11, figs. 3, 8; text-figs. 6, 7. (Sterile and fertile, sporangia, spores. Rhaetic and Lias; Greenland.)
 1932 *Todites williamsoni* (Brongn.): Oishi, p. 276, pl. 5, figs. 4–6. (Japan.)
 1932 *Todites roesserti* (Zeiller) Oishi, p. 274, pl. 4, figs. 7–9; pl. 5, figs. 1–3. (Japan.)
 1933 *Cladophlebis cf. whitbiensis* (Brongn.): Sze, p. 15, pl. 3, fig. 1 (left). (Sterile fragment. Japan.)
 ?1933 *Cladophlebis shansiensis* Sze, p. 13, pl. 3, figs. 1, 2. (Sterile leaf. China.)
 ?1933 *Cladophlebis fangtzuensis* Sze, p. 35, pl. 3, figs. 3, 4; pl. 4, fig. 6. (Sterile leaves. China.)
 1933a *Todites (Cladophlebis) cf. whitbiensis* (Brongn.): Sze, p. 9, pl. 6, figs. 3, 4. (Fertile pinnules. China.)
 1936 *Cladophlebis (Todites) cf. roesserti* Zeiller: P'an, p. 14, pl. 4, figs. 11–15; pl. 5, figs. 1–3. (Sterile. Keuper-Rhaetic; China. Certain other *Cladophlebis* leaves described by P'an are similar.)
 1937 *Todites williamsoni* (Brongn.): Brick, p. 8, text-fig. 2. (Fertile pinna. Central Asia.)
 1940 *Todites Goeppertianus* (Münster): Oishi, p. 194, pl. 3, fig. 1, 1a. (Fertile pinna. Japan.)
 1948 *Todites williamsoni* (Brongn.): Jones, p. 103, pl. 1, figs. 3, 4. (Sterile. Australia.)
 1950 *Todites goeppertianus* (Münster): Lundblad, p. 18, pl. 2, figs. 8–11. (Sterile and fertile pinnules, spores. Rhaetic; Sweden.)
 1950 *Todites goeppertianus* (Münster): Takahasi, p. 440, text-figs. 6, 7. (Sterile pinna. Trias; Japan.)

The following specimens figured under the names *williamsoni* and *whitbiensis* are considered distinct:

- 1876a *Asplenium whitbiense* Heer, pp. 38, 94, pl. 1, fig. 1 c; pl. 3, figs. 1–6; pl. 16, fig. 8; pl. 20, figs. 1, 6; pl. 21, figs. 3, 4 (fertile ?); pl. 22, figs. 4 G, 5C. (Sterile pinnae, veins different; fertile pinnae quite different. Amur Land.)
 1906 *Todites williamsoni* (Brongn.): Yokoyama, pp. 18, 20, 25, 28, pl. 3; pl. 5, fig. 1a; pl. 6, fig. 4; pl. 8, fig. 1. (Sterile pinnae. Jurassic; China.)
 1912 *Todites williamsoni* (Brongn.): Kryshfovich, p. 491, pl. 15, figs. 2, 2a, 3. (Sterile fragments. E. Urals.)
 1922 *Cladophlebis reversa* (Feistm.)=? *Todites williamsoni* (Brongn.): Seward & Holtum, p. 271, pl. 12, figs. 13, 15a, 15b, 16. (Indeterminable sterile fragments. Ceylon.)
 1925 *Cladophlebis (Todites) williamsoni* forma *whitbiensis* Kawasaki, p. 21, pl. 4, fig. 13. (Sterile, veins arising at larger angle. Korea. Ascribed to *C. haiburnensis* by Kawasaki, 1939.)
 1925 *Cladophlebis (Todites) williamsoni* (Brongn.): Kawasaki, p. 24, pl. 36, fig. 101. (Sterile, veins arising at larger angle. Korea. Ascribed to cf. *C. shansiensis* by Kawasaki, 1939.)
 1926 *Cladophlebis williamsoni* cf. *tenuicaulis* Kawasaki, pl. 7, fig. 21. (Veins at larger angle. Korea. Ascribed to *C. haiburnensis* by Kawasaki (1939).)

EMENDED DIAGNOSIS. Leaves usually wholly sterile or wholly fertile, but of similar size and shape. Leaf bipinnate, lamina as a whole long-lanceolate, apex acute, whole middle region of even width, base somewhat narrowed; lamina commonly 30 cm. broad and possibly 100 cm. long, but large leaves at least 60 cm. broad. Rachis typically 13 mm. (up to 2 cm.) broad, flattened or grooved above, rounded below. Pinnae arising at an angle of 75° and bending slightly backwards in lower part of leaf; at an angle of about 60° and straight over most of the

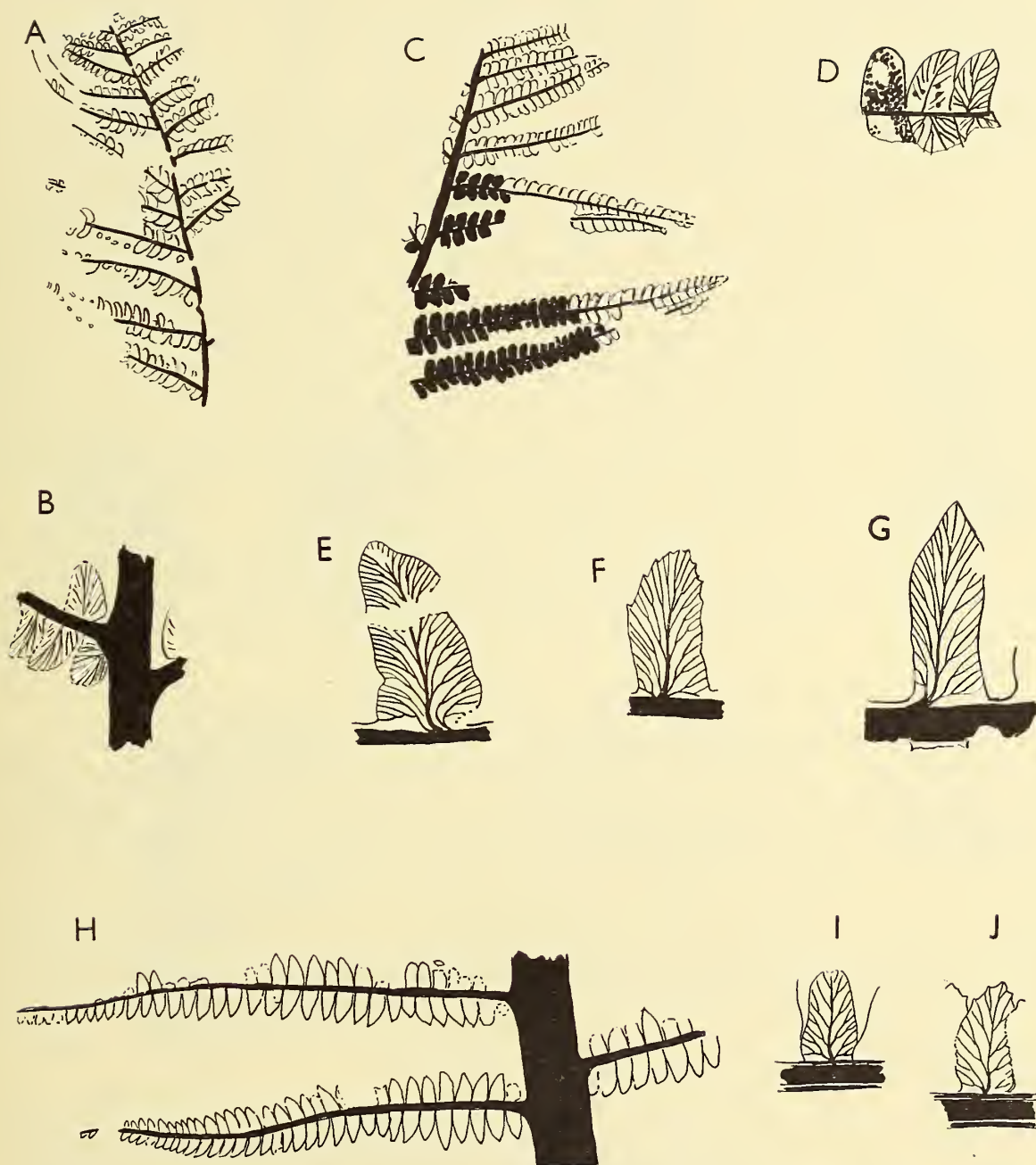


Fig. 28. *Todites williamsoni* (Brongniart)

A, near apex of sterile leaf with small pinnules, V.31464, $\times 1$. B, details from A, $\times 3$. C, near apex of partly fertile leaf with small pinnules (fertile pinnules in black), V.21404, $\times 1$. D, details from C, $\times 5$. E, venation of fertile pinnule (with apex of *next* pinnule drawn above it). V.31468, $\times 3$. F, denticulate form of sterile pinnule, V.31465, $\times 3$. G, elongated form of sterile pinnule from middle region of a leaf (main rachis 7 mm.), V.31467, $\times 3$. H, base of sterile leaf with small pinnules ($\frac{1}{3}$ omitted), K.406, Strickland Coll., Sedgwick Museum, Cambridge, $\times 1$. I, simple; and J, slightly denticulate pinnules from H, $\times 3$.

A, B, Cloughton Wyke *Solenites* Bed. C–G, Gristhorpe Bed. H–J, Yorkshire (imperfectly localised).

leaf and at 50° near the apex. Size of pinnae uniform over most of leaf, pinna rachis up to 2 mm. broad, somewhat channelled above. Surface of rachises without hairs. Pinna as a whole almost uniformly wide up to near its apex.

Pinnules differing considerably in different sterile leaves. In normal sterile leaves pinnules commonly arising at right angles to the rachis, the first always borne on the basiscopic side near the main rachis, but basal pinnules not specialised. Typical size of pinnule 8 mm. \times 3.5 mm., shape ovate-lanceolate, slightly curved forwards, basal margin usually contracted at pinna rachis, upper margin usually slightly expanded; lateral margins entire, apex acute. Pinnules usually separated by 1–2 mm. but occasionally in contact or overlapping. In certain sterile leaves pinnules larger, up to 15 \times 5.5 mm. In other sterile leaves pinnules smaller and down to 3.5 \times 2.5 mm. Shape of pinnules usually ovate-lanceolate when small but often irregularly lobed when large. In exceptional leaves some of the pinnules dentate near their apices. In leaves of all forms, shape of pinnules remains nearly uniform over three quarters of the length of pinna and then changes to a forward pointing acute angled triangle; near leaf apex pinnules becoming smaller. Lamina of pinnule not very thick, showing rather obscure sculpture of cellular pits, almost flat, without hairs on either side.

Midrib arising near basiscopic edge, first branch veins arising from its base or from the pinna rachis, forking 2–3 times. Next two pairs forked twice in well-developed pinnules, veins at first running near rachis but curving outwards and reaching margin at a concentration of 20–30 per cm. and at an angle of about 45° . Veins less branched but more crowded in small pinnules.

Fertile pinnules usually rather smaller than sterile, typical size in middle of leaf about 6 mm. \times 3 mm., but in large leaves up to 11 mm. \times 4 mm.; in others down to 3 mm. \times 2 mm. Shape when small, oval with a rounded apex but when large, lower margin contracted and lateral margins more or less lobed and apex obtuse. Fertile pinnules arising at right angles to the pinna rachis or even slightly reflexed; but bending forward; size and shape of adjacent pinnules often very uneven. Margins often slightly recurved, entire or with rounded lobes, never denticulate. Veins as in sterile pinnule but often more crowded and tending to curve outwards to meet the margin at about 70° . Sporangia usually covering whole under surface, borne in a single file along each vein. Sporangia ovoid, whole apical third of wall composed of thickened cells. Spores rounded, mean diameter 55μ , ranged noted 45μ – 75μ ; wall fairly thick and almost perfectly smooth. Triradiate crack nearly as long as spore radius, margins un-specialised. Number of spores per sporangium about 100.

DISTRIBUTION. *Todites williamsoni* is widespread and common in Yorkshire and occurs throughout the Deltaic series. Most of the finest specimens are from the Gristhorpe Bed where it is locally abundant. Apart from a possible extension below the Rhaetic, *Todites williamsoni* occurs as an abundant and widespread species from the Rhaetic, Lower Lias and probably continuously through the Lias to the Lower Oolite. It occurs in the Upper Jurassic (Kimeridgian) but probably not so commonly. It does not seem to be known from reliable specimens in the Cretaceous.

DISCUSSION. *Sporangia*. Raciborski (1894) and Zeiller (1903) gave good figures of sporangia of ferns of the *Todites williamsoni* group which proved that they agreed in several important features with the Osmundaceae and it seems to have been assumed that they were identical with those of *Todea* until Thomas (1911a: 385) pointed out a difference. Instead of a

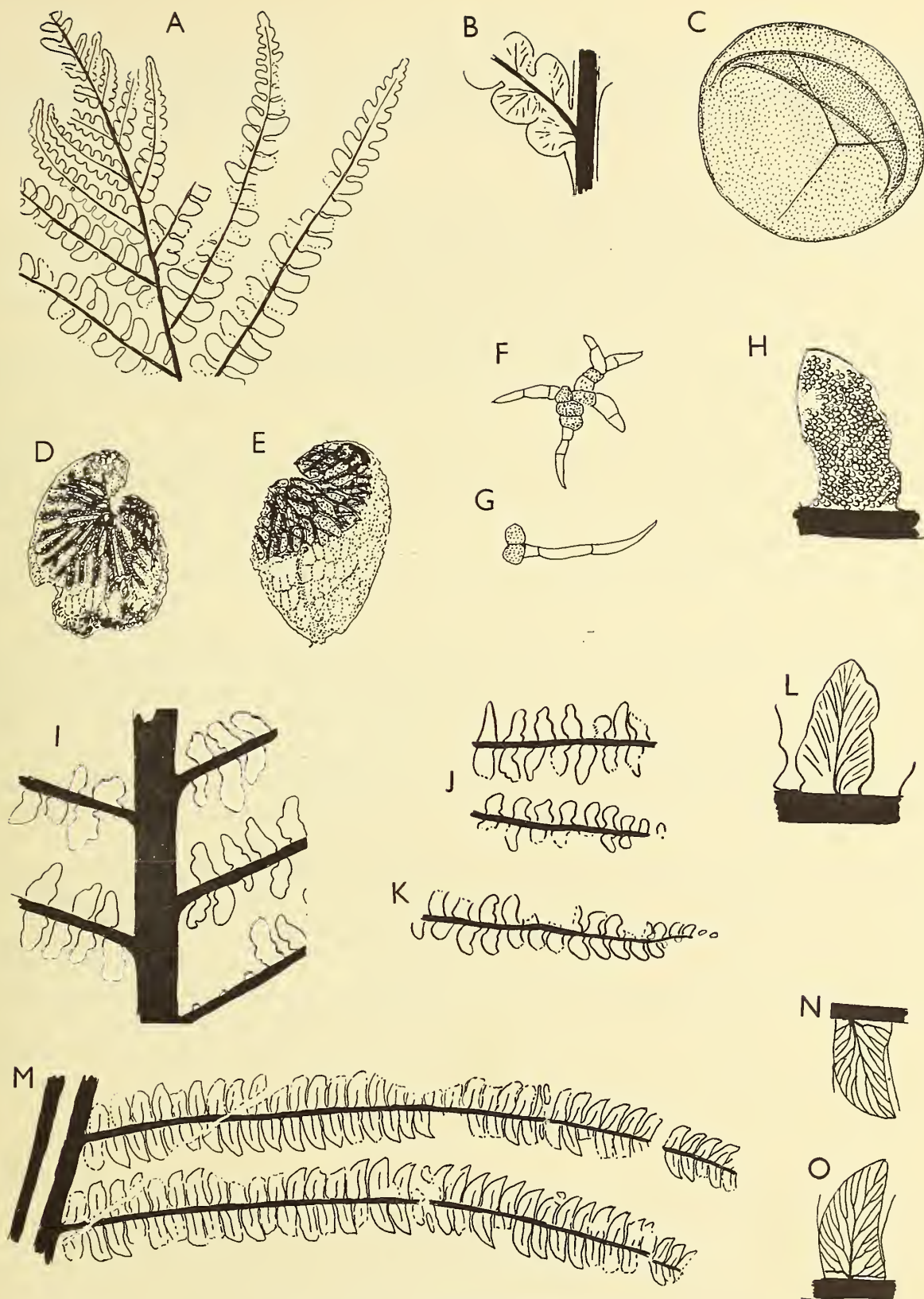


Fig. 29. *Todites williamsoni* (Brongniart)

A, apex of fertile leaf, J.5006, Oxford Museum of Geology, $\times 1$. B, details of A, $\times 3$. C, spore from V.28505, $\times 800$. D, E, dehiscent sporangia by transmitted light, in transfer, V.31468, $\times 60$. F, G, hairs among the sporangia, V.21414, $\times 100$. H, large fertile pinnule, J.5010, Oxford Museum of Geology, $\times 3$. I–L, portions of a large fertile leaf, V.2521. The pinnules in J begin 7 cm. from the rachis and in K about 10 cm. from the rachis, I–K, $\times 1$. L, details of a pinnule, $\times 3$. M, two pinnae from a large sterile slab. The rachis has split in preservation. K34, Leckenby Coll., Sedgwick Museum, Cambridge, $\times 1$. N, O, two pinnules of K34, $\times 3$. All are probably from the Gristhorpe Bed but A, H and M lack locality labels.

small lateral patch of thickened cells there is a large apical area of such cells which radiate from the top of the sporangium. This is well seen in Zeiller's figures but is even clearer in suitable transfers by transmitted light (Text-fig. 29 D, E). They thus agree with those of other fossil species.

Special peculiarities of this fern are:

(1) In about half the specimens the sporangia are still full of ripe spores.

(2) There are numerous filamentous branched hairs between the sporangia. These are scarcely to be seen in ordinary specimens unless exposed by transferring but are sometimes easily seen on the counterpart facing the sporangia when that is moistened with oil or transferred. No such hairs were seen in sterile parts of the leaf.

(3) The plane of cleavage often passes over the face of the sporangia, exposing them instead of the smooth back of the pinnule. I cannot explain this, but it is commoner when the sporangia are full than when they are empty.

The upper surface of the fertile pinnule is either smooth, apart from slight ridges along the veins, or else shows conspicuous dimples corresponding to sporangia. This effect is probably caused by collapse of the lamina into the sporangia during compression when the sporangia happen to face downwards.

Thomas (1911a) estimated the spore number at about one hundred. It has not been possible to make accurate counts, but I agree with his estimate.

Identification of the Sterile and Fertile Leaves. These were at first known as different species, the names *williamsonis* and *curtata* referring to fertile leaves and *whitbiensis*, *tenuis*, *recentior* and others to sterile leaves, but for many years they had been united under *williamsoni*. The evidence is (1) association in many different floras besides Yorkshire, (2) close agreement in everything but the shape of the pinnules, and (3) the fairly frequent production of partly sterile pinnules of intermediate form, or even of occasionally wholly sterile pinnules on otherwise fertile leaves. It is to be noted that Frenguelli (1947) rejects this identification in part.

Identification of various different shapes of Yorkshire leaf with one another. *Todites williamsoni* is one of the commonest Yorkshire species and there are some hundreds of specimens in Museums, about half of them fertile. There are many fine slabs some as much as 50 cm. long, and such pieces of leaves show that in any one leaf the pinnules whether sterile or fertile are, within the limits of certain variability between neighbours, nearly uniform throughout, except just at the leaf apex and ends of pinnae. It was earlier suggested (Harris 1931: 35) that there were two Yorkshire species one with larger and one with smaller pinnules than the Rhaetic *T. goeppertianus*, but despite vigorous efforts to divide the Yorkshire material into sharply defined species they are here accepted as growth forms of one species.

The evidence is as follows:

(1) Continuity of variation. The extreme forms not only intergrade but the intermediate forms are far commoner than the extremes.

(2) Distribution. The extreme forms occur together in each locality where the species is common. Different species on the other hand should have unrelated distribution.

(3) Microscopic features. Spores were prepared from every available specimen. They were all very similar indeed. It was noticed also that the peculiar hairs which cover the fertile pinnule are just the same on the largest and smallest forms.

Certain preparations gave spores of slightly greater mean size (about 65μ) than others, but this may be purely an effect of over-maceration, for the difference was noted between adjacent sporangia of the same pinnule. No general difference in size was found between the spores of the largest and smallest pinnules.

In addition to the variation in size of pinnules there is variability in texture, more delicate in some leaves than others. Certain specimens show remarkable unevenness of size of adjacent pinnules (Text-fig. 29 1), and this is not caused by damage in preservation since small size in one pinnule tends to be compensated by extra large size in the next. A very few sterile leaves show denticulate pinnules, such pinnules being adjacent to ordinary entire ones.

There is a marked tendency for large pinnules to be more lobed than small ones, but even this is not always true and some large ones do not even show the constriction at the basiscopic angle which is a feature of most of the Yorkshire specimens. I cannot explain this variability in pinnules, for leaves with small pinnules may show a thick rachis and also are just as often fertile as large and intermediate ones. It is, however, true that small pinnules occur in leaves with rather short pinnae (less than 15 cm. long) and large ones on long pinnae (up to 30 cm. long). Better material may prove the large pinnules to be usually on larger leaves.

Size of leaf. In the larger slabs the main rachis tapers by about 1 mm. in 20 cm. The largest rachis known in Yorkshire is about 18 mm. wide, but elsewhere there are rachises slightly exceeding 20 mm. Since the taper seems nearly uniform, the length of a large leaf should be several metres.

Comparison with material from other regions. Most authors distinguish the Middle Jurassic *Todites williamsoni* from the Rhaetic *T. goeppertianus*. Having now studied extensive and well-preserved material of the two species I reluctantly conclude that they can be distinguished only to an imperfect extent. That is to say, that a mixture of Greenland and Yorkshire specimens could be sorted into extreme forms with few errors, the Yorkshire ones with basally contracted pinnules, the Greenland ones with basally expanded pinnules, but the remainder (about half) would be indistinguishable. To separate groups overlapping to such an extent is not practical. In any case I suspect that this slight difference between these two populations does not separate the Rhaeto-Liassic from the Oolitic populations as a whole, for one extreme Yorkshire form with large, lobed pinnules occurs nowhere else. It is likely also that at Tonkin, the only other locality with abundant material, the range may again be slightly different from either for the combination of very long sterile and very short fertile pinnules is rather unusual.

The similar looking Keuper specimens (known by such names as *Acrostichites rhombifolius*) cannot be usefully discussed until better known.

Todites princeps (Presl) Gothan

Text-figs. 30, 31

1. Yorkshire specimens.

- 1835 *Pecopteris athyrioides* Brongniart, p. 360, pl. 125, fig. 3. (Sterile fragment, branching and venation similar.)
- 1864 *Sphenopteris modesta* Leckenby (ex Bean MS.), p. 79, pl. 10, fig. 3a, b.
- 1875 *Sphenopteris modesta* Leckenby: Phillips, p. 213, lign. 28, 29. (Sterile fragments.)
- ?1875 *Sphenopteris athyrioides* (Brongn.) Phillips, p. 212, lign. 27. (Sterile fragment.)
- 1900 *Sphenopteris princeps* Presl: Seward, p. 151, pl. 16, fig. 2. (Good sterile leaf.)
- 1913 *Todites williamsoni* (Brongn.): Thomas, pl. 23, fig. 6 only. (Sterile pinnule from Marske.)
- 1931 *Todites princeps* (Presl): Harris, p. 181, text-figs. 1-3. (Sterile and fertile leaves, sporangia, spores.)

2. Specimens from other regions.

- 1838 *Sphenopteris princeps* Presl in Sternberg, p. 126, pl. 59, figs. 12, 13. (Leafy stem. Lower Lias; Germany.)
 1838 *Germaria elymiformis* Presl in Sternberg, p. 188, pl. 59, figs. 1-9. (Rhizomes. Germany.)
 1838 *Pecopteris obtusata* Presl in Sternberg, p. 155, pl. 32, figs. 2a-c, 4a, b. (Leaf fragments. Germany.)
 1841 *Sphenopteris princeps* Presl: Goeppert, p. 72, pl. 10, figs. 3-7. (Germany.)
 1841 *Sphenopteris patentissima* Goeppert, p. 73, pl. 10, fig. 8. (Germany.)
 1867 *Acrostichites princeps* (Presl) Schenk, p. 46, pl. 7, figs. 3-5; pl. 8, fig. 1, 1a. (Good leaves and stems. Germany.)
 1890 *Sphenopteris princeps* Presl: Raciborski, p. 4, pl. 1, figs. 11-15. (Sporangia, see also 1894 below.)
 1890 *Todea princeps* (Presl) Raciborski, p. 9, pl. 1, figs. 10-13. (Small fragments. Lower Lias; Poland.)
 1894 *Todea princeps* (Presl): Raciborski, p. 18, pl. 6, figs. 22-27. (Good fertile pinnules and sporangia. Upper Lias; Poland.)
 ?1894 *Todea* sp., Raciborski, pl. 7, figs. 4-6c, 7, 8. (As 1890 above.)
 1902 *Acrostichites princeps* (Presl): Möller, p. 26, pl. 2, fig. 19. (Small leaf. Liassic; Bornholm.)
 1903 *Sphenopteris* cf. *princeps* Presl: Zeiller, p. 23, pl. 1, figs. 1, 2. (Sterile fragment. Tonkin.)
 1907 *Sphenopteris princeps* Presl: Seward, p. 27, pl. 5, figs. T, U, pl. 6, figs. 42, 43. (Good sterile leaves. Jurassic; Russia.)
 1911 *Sphenopteris modesta* Leckenby: Seward, p. 42, pl. 2, figs. 18, 18a, 19; pl. 5, fig. 63; pl. 6, fig. 70. (Excellent sterile leaves. China.)
 1914 *Todites princeps* (Presl): Gothan, p. 95, pl. 17, figs. 3, 4. (Sterile leaf. Lower Lias; W. Germany.)
 1926 *Todites* cf. *princeps* (Presl): Harris, p. 56, pl. 12, fig. 5; text-fig. 2 A-E. (Sterile and fertile fragments, sporangia. Greenland.)
 1931 *Todites princeps* (Presl): Harris, p. 35, pl. 11, figs. 1, 2, 4, 9; pl. 12, fig. 3; text-figs. 8, 9. (Good sterile and fertile leaves. Greenland.)
 1932 *Todites princeps* (Presl): Oishi, p. 279, pl. 23, fig. 7. (Good sterile leaf. Rhaetic; Japan.)
 1937 *Todites princeps* (Presl): Harris, p. 15. (Discussion of age in Greenland.)
 1937 *Todites princeps* (Presl): Brick, p. 9, pl. 2, figs. 1-11; text-fig. 3. (Good sterile and fertile leaves; veins. Central Asia.)
 1939 ?*Sphenopteris princeps* Presl: Kawasaki, p. 23, pl. 8, fig. 37. (Sterile leaf. Korea.)
 1941 *Todites princeps* (Presl): Brick, p. 15, pl. 5, fig. 1. (Sterile fragments. Central Asia.)
 1949 *Sphenopteris modesta* Leckenby: Sze, p. 8, pl. 1, figs. 1-3; pl. 8, fig. 7; pl. 13, fig. 8. (Good leaves. Hupeh, China.)
 1957 *Todites princeps* (Presl): Stanislavski, p. 29, pl. 4, fig. 6; text-fig. 5. (Sterile fragments. S. Russia.)

EMENDED DIAGNOSIS. Sterile and fertile leaves similar, petiolate. Lamina as a whole long-lanceolate, gradually narrowed towards both ends. Size up to about 80 cm. or possibly 100 cm. \times 15 cm., but sterile leaves often much smaller. Petiole and rachis up to 3 mm. thick, rounded in section, surface bearing stiff backward pointing hairs. Pinna rachises bearing smaller outward pointing hairs, midribs of pinnules bearing still smaller forward pointing ones. Hairs simple, arising from a thickened base, tapering to a sharp point, composed of about six cells.

Pinnae usually almost opposite. Basal pinnae short, pointing rather backward. Middle pinnae arising almost at right angles to the rachis, upper ones at an angle of 70°-80°. Pinnules often slightly larger on lower side of pinna than on upper. Basal pinnules opposite except in the smallest pinnae, later ones gradually becoming alternate with the earlier ones on the acroscopic side (anadromic branching). Basal pinnules unspecialised, but often lying partly over the main rachis. Pinnules in large leaves oblong, 10 mm. \times 3 mm. subdivided almost to the midrib into notched or truncate lobes. Pinnules in medium sized leaves about 6 mm. \times 2.5 mm., partly divided into rounded lobes about 1 mm. broad; pinnules in small leaves (and near apex of large ones) relatively shorter, oval with obtusely dentate margins. Pinnules in smallest leaves 1 mm. long and 1 mm. broad, margins entire. Lamina in all sterile and many

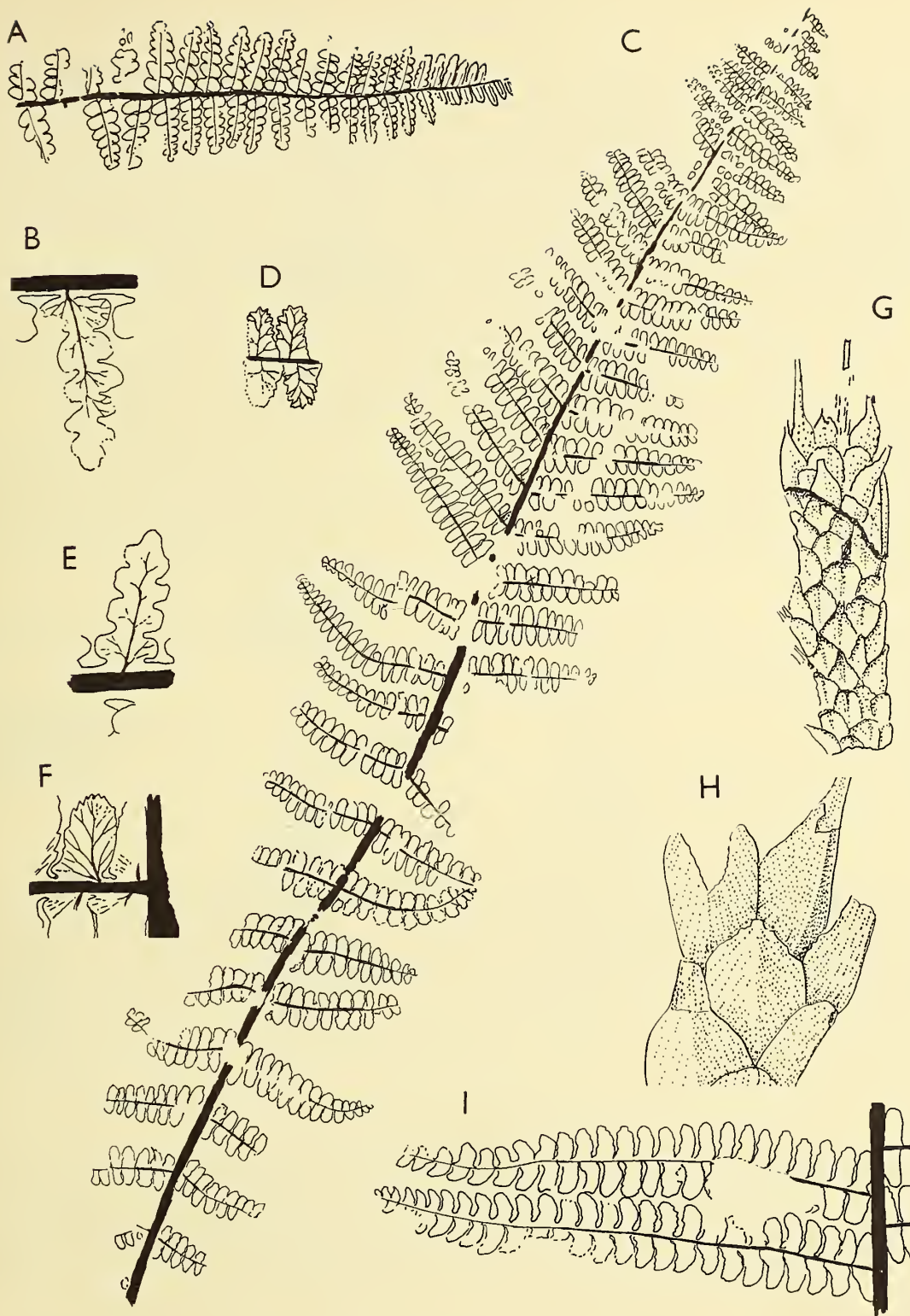


Fig. 30. *Todites princeps* (Presl), sterile leaf

A, isolated pinna of large leaf, V.31476, $\times 1$. B, pinnule of another pinna associated with A, $\times 3$. C, almost complete leaf of rather small size. Leckenby Coll. 150, Sedgwick Museum, Cambridge, $\times 1$. D, pinnules from middle of C (at point marked X), $\times 3$. E, single pinnule from a moderate sized isolated pinna, V.31477, $\times 3$. F, single pinnule from the top of the leaf shown in I, $\times 3$. G, rhizome, the upper part shows the fossil, the lower part the imprint, V.32061, $\times 1$. H, details from counterpart of G, $\times 3$. I, two pinnae of a moderate-sized leaf (most of specimen omitted). Leckenby Coll. 155, Sedgwick Museum, Cambridge.

A, B, G, H, are from Haiburn Wyke *Zamites* Bed. C, D, F, I, unlocalised, ? Haiburn Wyke. E, Beast Cliff Fern Bed.

fertile leaves continuous as a flange 0.5 mm. wide along the pinna rachis and upper parts of the main rachis. Substance of lamina very delicate but more than one cell thick.

In largest pinnules, midrib median, giving off lateral veins at a wide angle. Lowest pair of veins and lowest lobes of pinnule nearly opposite, but upper ones becoming alternate, the lobes on the main rachis side being broader and therefore drawing ahead (anadromic branching). Venation of lobes nearly dichotomous, veins usually branched twice. In smaller pinnules, midrib tending to be nearer the main rachis, first branch arising on the acroscopic side and forking twice to supplying the large basal lobe, other branches forked once. All branch veins reaching the margins. Surface of small pinnules flat, but surface in larger pinnules often crisped with margins of lobes curved downwards. Pinnules often crowded and with the large forward pointing basal lobe overlapping the next pinnule.

Fertile leaf similar to larger sterile leaves. Weakly fertile pinnules bearing a few sporangia along the main veins but not otherwise modified. Fully fertile pinnules crowded with sporangia along the veins. Sporangia oval $250\mu \times 150\mu$, with an apical cap of thickened cells and dehiscing by a longitudinal crack. Spores probably 50–100 per sporangium. Spores round, about 32μ wide (20μ – 40μ) with a thin smooth wall. Triradiate cracks finely marked, rather shorter than the spore radius.

DISTRIBUTION. *T. princeps* is locally common in Yorkshire at Gristhorpe, in the Haiburn Wyke plant bed and the Beast Cliff fern bed. All the older figured specimens seem to be from Gristhorpe or Haiburn. Its localities are distributed as follows:

Upper Deltaic	1 loc. (M. Black, No. 712 in Sedgwick Museum)
Middle Deltaic Gristhorpe Series	1 or possibly 2 locs.
Middle Deltaic Sycharham Series	1 loc.
Lower Deltaic	5 locs.

Elsewhere it is widespread in the European Lower Liassic. It occurs in some abundance in W. Germany (Presl in Sternberg, 1938; Göppert, 1841; Schenk, 1867; Gothan, 1914) Poland (Raciborski, 1890), and it also occurs in the Lower Liassic of East Greenland (Harris, 1926, 1931) and in rocks perhaps of this age in Japan (Oishi, 1932, 1940). The specimen from Tonkin (Zeiller, 1903) may be of Rhaetic Age. (The European ones formerly regarded as Rhaetic all appear to be Lower Liassic.) In Poland again (Raciborski, 1894) it occurs in Middle Jurassic rocks (? Upper Liassic); but it is nowhere known from rocks younger than the Inferior Oolite of Yorkshire. The specimens from the Inferior Oolite have usually been identified with the Liassic ones, but intermittently have been distinguished (Seward, 1911) under Leckenby's specific name *Sphenopteris modesta*. Having studied many Liassic specimens from Greenland and from the Yorkshire Oolite it can be stated that their agreement appears to be perfect in every known respect; both collections include specimens which vary in size and form but each form of one matches the other. If they are to be separated the distinguishing character has not yet been discovered.

DISCUSSION. This elegant fern forms a most satisfactory species, even small fragments being recognisable by the anadromic branching of the pinnules and veins, so far a unique feature among Jurassic ferns of this general appearance. Many specimens have been examined and no exception has been found (though it is difficult to say which is the top of certain small pieces). See also Fig. 50K.

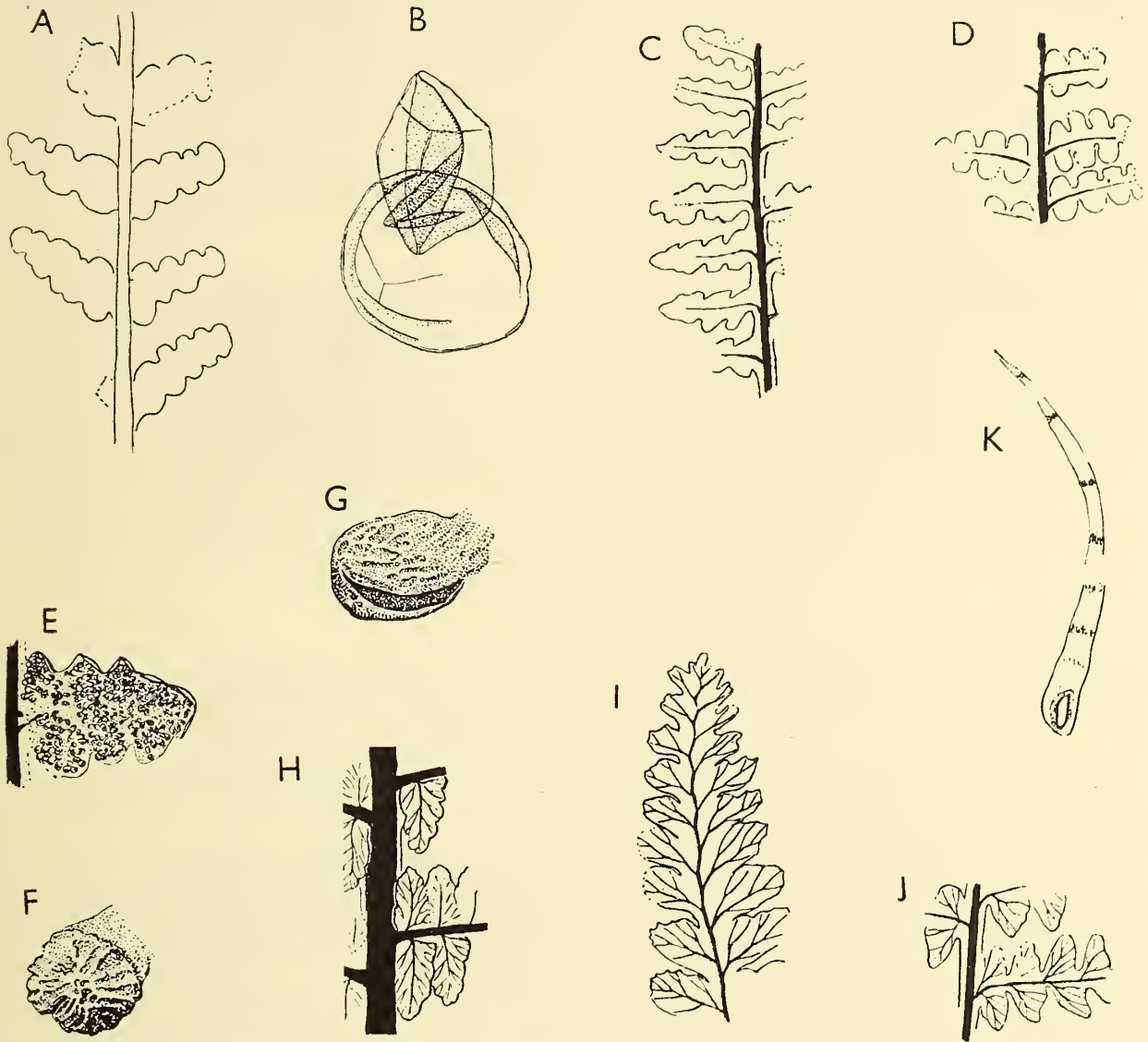


Fig. 31. *Todites princeps* (Presl)

A, fertile pinna, J.5027, Oxford Museum of Geology, $\times 2$. B, two spores from a spore mass; both show triradial scars. Specimen Z, Yorkshire Museum, $\times 800$. C, fertile pinna, the margins of the lobes are recurved. Specimen Y, Yorkshire Museum, $\times 2$. D, fertile pinna with strongly lobed pinnules. V.27428, $\times 2$. E, transfer of fertile pinnule showing the general distribution of the sporangia (individual sporangia not all clear enough for accuracy). Specimen Z, Yorkshire Museum, $\times 5$. F, thickened cells from the end of a sporangium in transfer. Same specimen as E, $\times 100$. G, opening of a sporangium from same specimen, $\times 100$. H, pinnules from the middle region of a medium sized leaf, J.5021, $\times 2$. I, apical region of a pinna, J.5056, $\times 4$. J, pinnules from the apical part of a leaf, J.5056, $\times 4$. K, hair from a pinna rachis; transfer preparation, J.5048, $\times 40$.

A, ? Gristhorpe Bed. C, D, Gristhorpe Bed, the rest are imperfectly localised. All figures are from Harris (1948, text-figs. 2, 3).

The variation in size of the leaf is rather unusual but causes no great difficulty because leaves of different sizes are usually found together, and the identity of the different sizes has long been recognised. The strange feature is the relative abundance of rather small leaves; these are actually commoner than full-sized ones. No complete specimen of a large leaf has been obtained and the length given is merely an estimate. Fully fertile leaves are rather rare and in almost all of these the sporangia are empty and the only full ones so far obtained are those from a specimen in the Yorkshire Museum.

In an earlier account (Harris, 1948: 189) reference was made to the hairs on the main rachis as pointing forwards. This is now corrected.

T. princeps agrees in its apically thickened sporangia with other species of *Todites* rather than with *Todea* or *Leptopteris*. Apart from this it rather suggests *Leptopteris* in the fairly small size of the leaf, the delicate texture of the lamina and the strong tendency of the pinnae to be sub-opposite rather than alternate (in about four specimens out of five). This feature is shown also in many herbarium sheets at the British Museum representing the Recent species *L. fraseri* *L. moorei* *L. wilkesiana* and *L. hymenophylloides*. In two *L. superba* and *L. alpina* there is no tendency for them to be opposite, nor is there in *Todea barbara*. The branching is, however, dissimilar for in every one of these species where it could be seen it is katadromic, just as in *T. barbara*. Clearly then, *Todites princeps* only approaches *Leptopteris* in a few characters.

Rhizome. The specimen shown in Text-fig. 30 G, H is the best of a series of rhizome fragments which occur in a layer of the Haiburn *Zamites* Bed full of sticks and petioles. It shows spirally arranged leaf bases from which arise slender petioles; the leaf bases are expanded and their conspicuous cells converge on the petiole. Their direction is suggested by the stippling.

The margins, and to some extent the abaxial sides, of the petiole bases are covered with straight, tapering hairs about 1 mm. long.

The specimen has been identified with *Todites princeps* because: 1. Similar rhizomes, some identified by continuity with small leaves, are known from the Lower Lias of W. Germany (Presl in Sternberg, 1838), leafy ones as *S. princeps* leafless ones as *Germaia elymiformis* (see also Schenk, 1867). 2. The present leafless specimens bear hairs which are similar to those on the leaf rachis, though rather larger. Leaves of *T. princeps* are among the ferns associated with them. The epidermis is quite uncutinised and almost rules out a Gymnospermous origin for this stem. 3. Broadly expanded leaf bases are typical of the Osmundaceae but apparently do not occur in other Leptosporangiate ferns.

The fact that several rhizomes of this fern are now known from two floras requires explanation, for fern rhizomes are in general rare. Possibly this fern may be an epiphyte and, if so, the whole plant could rather easily fall and be swept by water into the pools where preservation occurred. This would rarely happen in land growing plants.

COMPARISON. Fragments of this fern can resemble fragments of various other finely divided leaves for example *Coniopteris hymenophylloides* and *K. arguta*. In every case careful examination of the branching of veins and pinnules distinguishes them. The bristles on the rachis are another valuable distinguishing character; they are usually seen easily when the impression of the rachis is moistened with oil.

There is little doubt that *Pecopteris athyrioides* Brongniart (1835) is the same as *T. princeps* and hence is the earliest name. The specimen should be re-examined.

Genus OSMUNDOPSIS Harris

1931a *Osmundopsis* Harris, p. 136 (nomen nudum).

1931 *Osmundopsis* Harris, p. 48. (Diagnosis.)

EMENDED DIAGNOSIS. Sterile and fertile leaves dimorphic. Sterile leaf bipinnate, a *Cladophlebis*. Fertile leaf as a whole lanceolate, bipinnate or tripinnate with no lamina, ultimate branches filiform, bearing groups of sporangia. Sporangia pear-shaped, whole apical region of wall thickened, dehiscence by a longitudinal stomium. Spores rounded with triradiate scars.

DISCUSSION. *Osmundopsis* agrees with *Osmunda* in all known characters but two; the leaves are dimorphic and the sporangia have a relatively larger area of thickened cells. Raciborski (1894) recognised the first of these characters in his *Osmunda sturi*, the second is noted here. It is possible that these differences are insufficient to differentiate a valid genus but in any case the name *Osmundites* is inadmissible since it refers to fossils of a different category (petrified stems).

TYPE SPECIES. *Osmundopsis sturi* (Raciborski).

Osmundopsis sturi (Raciborski) Harris

Text-fig. 32

1894 *Osmunda Sturii* Raciborski, p. 161, pl. 6, figs. 7, 9–16; pl. 11, fig. 7b. (Also probably '*Osmunda* sp.', pl. 6, fig. 8: Good figures of fertile pinnae and sporangia. Poland.)

1931 *Osmundopsis sturi* (Raciborski) Harris, p. 48.

EMENDED DIAGNOSIS. Fertile leaf as a whole probably lanceolate with a smooth, slender rachis channelled above, bearing slender primary branches at a wide angle; secondary branches patent, rather crowded, up to 10 mm. long, very slender. Tertiary branches minute or suppressed, but covered with sporangia. Sporangia crowded, pyriform or obovate about 0.6 mm. × 0.4 mm. Cells of whole apical region thickened. Spores numerous, round, about 40μ wide, with tuberculate walls and well-marked triradiate cracks; margins of cracks scarcely thickened. (Sterile leaf unknown.)

This diagnosis is based partly on that of Raciborski and partly on the present material.

DISCUSSION. *Osmundopsis sturi* is represented by only two Yorkshire specimens. Both are minute fragments from the Gristhorpe Bed (Middle Deltaic). In one all sporangia have dehisced, but the other has some still full. It was not found possible to disintegrate the spore masses for a spore count. It is, however, clear that the number is large, certainly more than 100, and possibly rather more than 200. This species deserves further study. Its sterile leaf has yet to be recognised and even the fertile leaf is very incompletely known.

COMPARISON. The Yorkshire fragments agree fully with the rather better Polish originals of *O. sturi* if some allowance is made for the different method of preparation (the wall cells of the sporangia are only seen clearly in transfers). They differ from the other described species, but the determination of such limited material is necessarily rather insecure.

The other species are *O. microcarpa* Raciborski (1894: 163, pl. 6, fig. 21) which is too little known for any comparison; *O. plectrophora* Harris from the Lower Lias of Greenland which has longer stalked sporangial groups and rather broader sporangia. *Osmundites prigorovskii* Kryshtofovich & Prinada (1933) is perhaps similar but the illustrations do not exclude the

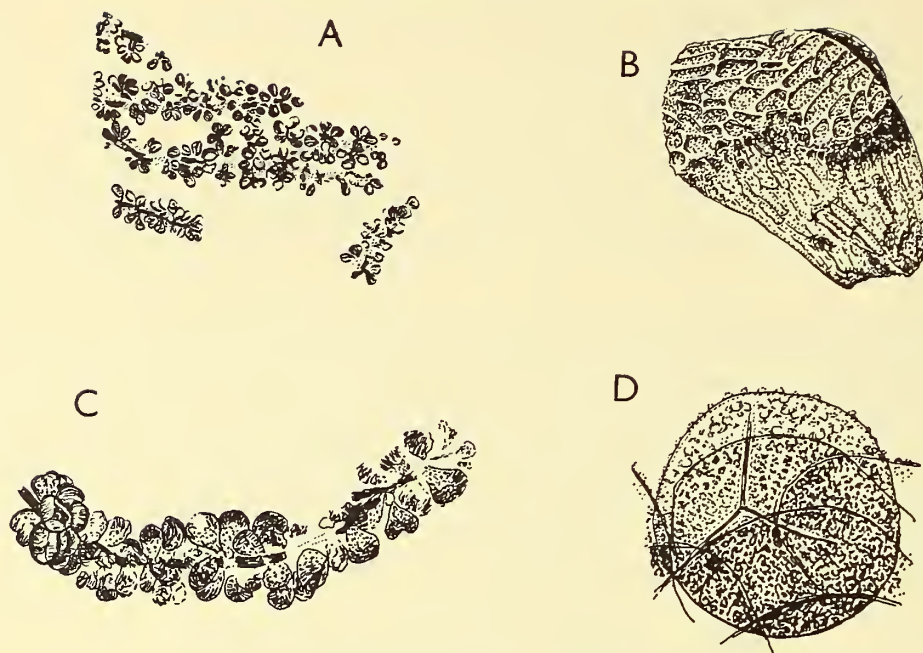


Fig. 32. *Osmundopsis sturi* (Raciborski)

A, fertile segments, V.28651, $\times 4$. B, single sporangium from C, $\times 60$. C, isolated fertile segment, V.31979, $\times 10$. D, spore at edge of spore mass, from A, $\times 800$. Both specimens from Gristhorpe Bed.

possibility that it is a *Todites* of the *Cladotheca* group. *O. plectrophora* of Brick (1935) and *O. subplectrophora* of Oishi & Huzioka (1938) are sterile leaves and thus not comparable with the present material.

Family MATONIACEAE

Genus PHLEBOPTERIS Brongniart, 1836:371

(*Laccopteris* of many authors)

Hirmer & Hoerhammer (1936) discussed this genus in their comprehensive revision of the fossil Matoniaceae. One of their general conclusions (on the fundamental leaf architecture) appears still open (see Lundblad 1950) but it is not discussed here since the Yorkshire specimens provide no evidence. The other, on the relation of *Phlebopteris* to *Nathorstia* affects the taxonomic treatment of this flora profoundly.

The Cretaceous fern *Nathorstia* Heer is usually regarded as Marattiaceous with *Kaulfussia*-like synangia entirely different from the ring of free sporangia in *Phlebopteris*, but Seward and others have doubted the distinction, believing that *Nathorstia* is merely *Phlebopteris* with closely and regularly packed sporangia. The difficulty is illustrated in Hirmer's treatment; in 1927 he included all of *Nathorstia* in *Laccopteris* (*Phlebopteris*), but in 1936 Hirmer & Hoerhammer revived *Nathorstia* and included in it many species which had hitherto always been referred to *Phlebopteris*. This kind of uncertainty is to be expected with closely

allied genera and with those which are very little known, but is repugnant where they are supposedly very different and well known. Miner (1935) who described a typical looking Cretaceous '*Nathorstia*' as *Laccopteris* returned to Hirmer's 1927 position. The agreement between the sorus figured by Miner (1935, pl. 1, fig. 3) and that of Hirmer & Hoerhammer (1936, pl. 5, fig. 5) is impressive. I have also been impressed by Schenk's drawings (1875, pl. 28, figs. 11a, b) of the sorus of *P. dunkeri* one of the species later included by Hirmer & Hoerhammer (1936) in *Nathorstia*.

I conclude that all the species described here are true *Phlebopteris*, and that the type species of *Nathorstia* deserves re-examination. It should be possible to obtain conclusive evidence from balsam transfers of old and empty fructifications, for the sporangia usually fall off from the placenta in *Phlebopteris* while in *Kaulfussia* the empty synangial wall lasts indefinitely.

The limits of the genera *Phlebopteris*, *Matonidium* and *Matonia* prove less clear cut than had been supposed. They appear to intergrade. No changes, however, have been made in the customary genus of the species described here.

Key to the Yorkshire Matoniaceae

- | | |
|--|-----------------------------------|
| (1) Vein branches all free | 2 |
| Vein branches anastomosing | 4 |
| (2) Veins simple or forked once | 3 |
| Veins forked twice or more | <i>Phlebopteris woodwardi</i> |
| (3) Veins at angle of less than 45° to midrib | <i>Selenocarpus</i> |
| Veins at an angle of more than 45° to midrib | <i>Matonidium</i> |
| (4) Primary vein arch flattened and bearing sorus | <i>Phlebopteris polypodioides</i> |
| Primary vein arch raised and enclosing sorus | 5 |
| (5) Primary vein arch enclosing 1 soral vein but no others | <i>Phlebopteris woodwardi</i> |
| Primary vein arch enclosing many small veins | <i>Phlebopteris dunkeri</i> |

The following additional characters are sometimes diagnostic:

Matonidium goepperti: Large (50μ) thick walled spores; indusium.

Phlebopteris polypodioides: Hairs on under side of pinna rachis.

Phlebopteris woodwardi: Thick lamina, strong bulge above sorus, outer veins parallel or vein meshes elongated.

Phlebopteris dunkeri: Vein meshes very small, nearly isodiametric.

Selenocarpus: Pinnules contracted basally.

Phlebopteris polypodioides Brongniart

Text-figs. 33, 34

1. Yorkshire specimens.

- 1828 *Phlebopteris polypodioides* Brongniart, p. 57. (Nomen nudum.)
- 1829 *Pecopteris caespitosa* Phillips, p. 148, pl. 8, fig. 10. (Rough sketch of leaf base redrawn in Seward, 1900, text-fig. 8.) Identified by Hirmer & Hoerhammer (1936: 7) with *Phlebopteris brauni* and with *Matonidium* (p. 42). Specimen in York Museum.
- 1829 *Pecopteris crenifolia* Phillips, p. 148, pl. 8, fig. 11, 11a. (Fertile pinna, edges appearing waved. Specimen in York Museum.)
- 1833 *Pecopteris polypodioides* (Brongniart) Lindley & Hutton, p. 167, pl. 60. (Fertile pinna, veins shown imperfectly. No. 618.39 Scarborough Museum.)
- 1834 *Pecopteris propinqua* Brongniart: Lindley & Hutton, p. 101, pl. 119. (Fertile pinna. Margin appears lobed, possibly imperfectly prepared.)
- 1835 *Phlebopteris contigua* Lindley & Hutton, p. 177, pl. 144. (Sterile pinna, venation.)

- 1836 *Phlebopteris polypodioides* Brongniart, p. 372, pl. 83, fig. 1, 1A. (Good fertile pinna.)
 1836 *Phlebopteris propinqua* (Brongn.) Brongniart, p. 373, pl. 132, fig. 1; pl. 133, fig. 2. (Same figures as Phillips' *P. crenifolia* and Lindley & Hutton's pl. 119.)
 1836 *Hemitelites polypodioides* (Brongn.) Goeppert, p. 336, pl. 15, figs. 8, 9. (Brongniart's specimen refigured.)
 1875 *Phlebopteris polypodioides* Brongn.: Phillips, p. 202, lign. 10. (Venation of fertile pinnule.)
 1875 *Pecopteris crenifolia* Phillips: Phillips, p. 202, pl. 8, fig. 11, 11A. (As 1829.)
 1899 *Laccopteris polypodioides* (Brongn.) Seward, p. 197, text-fig. 9 B. (Venation of fertile pinnules.)
 1900 *Laccopteris polypodioides* (Brongn.): Seward, p. 78, pl. 12; pl. 13, figs. 1, 2; text-figs. 8, 10, 11 B (as 1899), not figs. 9, 11 A, C. (Good sterile and fertile leaves, sorus, veins.)
 1910 *Laccopteris polypodioides* (Brongn.): Seward, p. 358, text-figs. 266, 267 B (as Seward, 1900, text-figs. 10, 11 B). (Not text-fig. 268 = *Annulariopsis*.)

The following is regarded as distinct:

- 1829 *Pecopteris ligata* Phillips, p. 148, pl. 8, fig. 14. (Figure looks different but *Phlebopteris polypodioides* according to Nathorst, 1880.)

2. Specimens from other regions.

- 1835 *Phlebopteris schouvi* Brongniart, p. 374, pl. 132, figs. 4, 4a, 5, 6. (Sterile and fertile fragments. Bornholm.)
 1865 *Phlebopteris polypodioides* Brongn.: Heer, p. 80, pl. 4, fig. 8. (Fragment. Lower Lias; Switzerland.)
 1867 *Phlebopteris affinis* Schenk, p. 62, pl. 13, fig. 1, 1a, b. (Sterile and fertile fragments, veins. Lower Lias; W. Germany.)
 1869 *Phlebopteris affinis* Schenk: Schimper, p. 624, pl. 39, figs. 14-16 (as Schenk, 1867.)
 1877 *Phlebopteris affinis* Schenk: Heer, p. 126, pl. 51, fig. 8. (As Heer, 1865.)
 1892 *Phlebopteris affinis* Schenk: Bartholin, p. 24, pl. 9, figs. 4-5a. (Fragments. Lower Lias; Bornholm.)
 ?1892 *Laccopteris* n. sp., Bartholin, p. 22, pl. 10, fig. 1, 1a. (Fertile pinna. Lower Lias; Bornholm.)
 1902 *Phlebopteris affinis* Schenk: Möller, p. 38, pl. 3, fig. 19. (Sterile pinnule. Lower Lias; Bornholm.)
 1902 *Microdictyon woodwardi* (Leckenby): Möller, p. 39, pl. 4, figs. 2-4. (Sterile pinnules. Lower Lias; Bornholm.)
 1906 *Laccopteris polypodioides* (Brongn.): Krasser, p. 593, pl. 1, fig. 12. (Lower Jurassic; Manchuria.)
 ?1913 *Laccopteris* sp., Möller & Halle, p. 14, pl. 2, figs. 9, 10. (Sterile fragment with similar venation. Lower Lias; Sweden.)
 ?1920 *Laccopteris polypodioides* (Brongn.): Yabe, pl. 2, fig. 1. (China.)
 1925 *Laccopteris polypodioides* (Brongn.): Kawasaki, p. 9, pl. 11, figs. 39-41; pl. 12, fig. 42; pl. 34, fig. 94. (Sterile and fertile pinnae. Lower Jurassic; Korea.)
 ?1926 *Laccopteris polypodioides* (Brongn.): Moisseiev, p. 585, pl. 10, figs. 8, 9. (Details obscure. Russia.)
 1929 *Laccopteris polypodioides* (Brongn.): Edwards, p. 390. (No figure, photographs in British Museum. Inferior Oolite; Sardinia.)
 1931 *Laccopteris affinis* (Schenk) Harris, p. 77, text-fig. 27. (Sterile pinnae. Rhaetic; Greenland.)
 1936 *Phlebopteris polypodioides* Brongn.: Hirmer & Hoerhammer, p. 34, pl. 7; text-figs. 2, 5. (Good sterile and fertile leaves from Rhaetic of Germany.)
 ?1939 *Laccopteris polypodioides* (Brongn.): Kawasaki, p. 12, pl. 8, figs. 34, 35. (Sterile fragments, no details. Korea.)
 1942 *Phlebopteris affinis* Schenk: Teixeira, p. 10, pl. 1, fig. 8; text-fig. 6. (Sterile fragments. Upper Trias or Lower Lias; Portugal.)
 ?1949 *Laccopteris* cf. *polypodioides* (Brongn.): Sze, p. 5, pl. 13, figs. 1, 2. (Fertile fragments. Hupeh. China.)
 1950 *Phlebopteris polypodioides* Brongn.: Lundblad, p. 24, pl. 3, fig. 7; text-figs. 5A, 6. (Good pinnae. Rhaetic; Sweden.)
 1950 *Phlebopteris* sp., Lundblad, p. 25, pl. 3, figs. 8, 9; text-fig. 5 B. (Pinna fragments. Rhaetic; Sweden.)

The following are distinct:

- 1888 *Phlebopteris alethopteroides* Etheridge, p. 1306, pl. 38, figs. 1, 2. (Australian specimens with rather different venation, included by Hirmer & Hoerhammer, 1936.) See Walkom (1917: 8).
 1902 *Laccopteris polypodioides* (Brongn.): Möller, p. 31, pl. 2, figs. 25, 26. (= *P. angustiloba*. Bornholm.)
 1927 *Laccopteris* sp., Carpentier, p. 26, pl. 3, figs. 6, 7. (Wealden fragments included by Hirmer & Hoerhammer, 1936. France.)
 1937 *Laccopteris polypodioides* (Brongn.): Brick, p. 12, pl. 1, figs. 1, 2. (Venation different. Central Asia.)

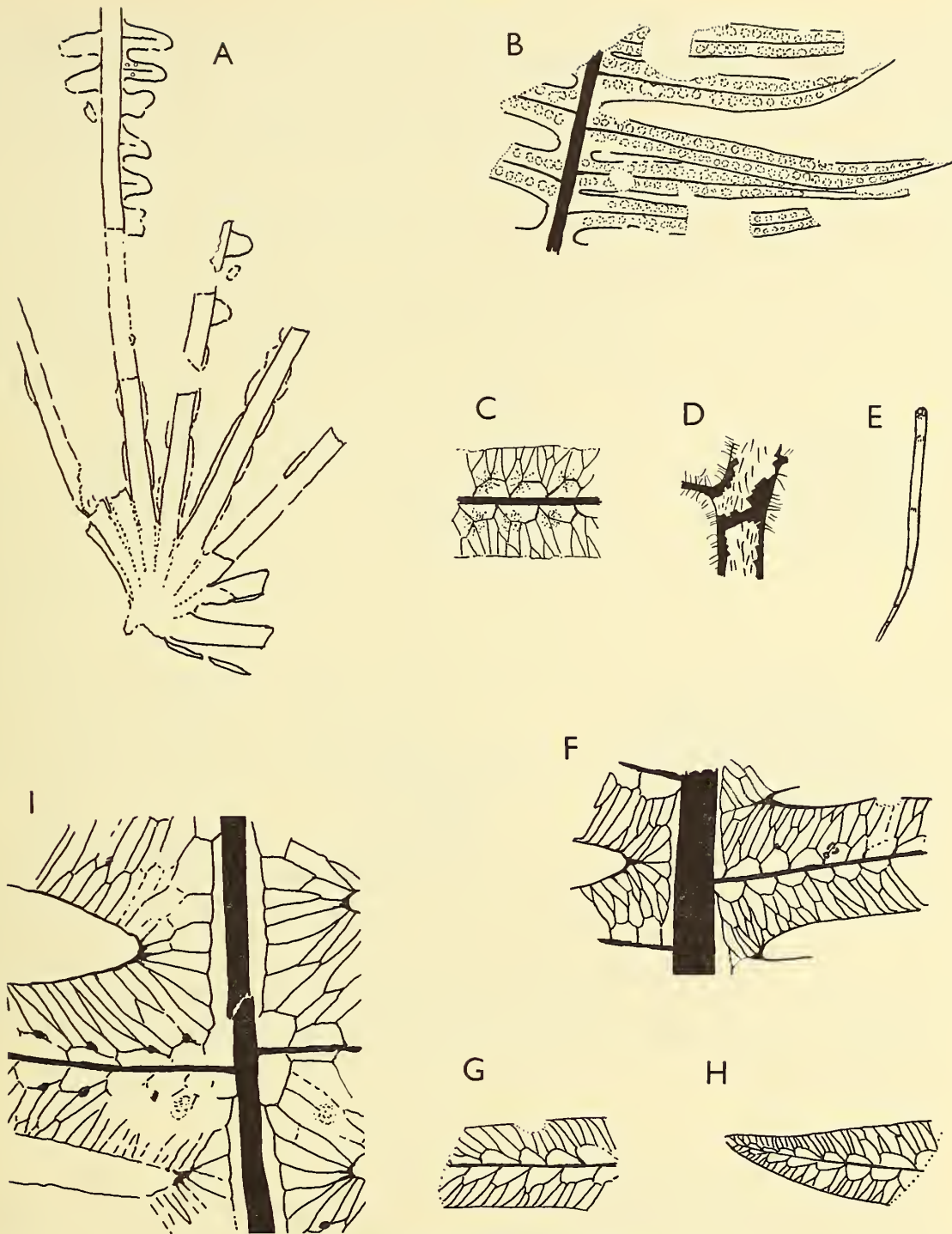


Fig. 33. *Phlebopteris polypodioides* Brongniart

A, part of the base of a full sized leaf. Leckenby Coll., 130, Sedgwick Museum, Cambridge, $\times 1$. B, typical fertile pinna. Leckenby Coll., 131, $\times 1$. C, details of B, $\times 3$; the sori are only seen as indistinct imprints. D, hairs on underside of pinna rachis and midrib, V.25886, $\times 4$. E, one of the reflexed hairs from D, $\times 50$. F, venation of V.25886, there are the remains of three sporangia near the second placenta on the right, $\times 3$. G, H, outer parts of pinnae of V.25886, $\times 3$. I, specimen with unusually broad pinnules (preserved in ironstone). V.3666, $\times 3$.

A-C, imperfectly localised. D-I, Gristhorpe Bed.

DIAGNOSIS. Main rachis up to 1 cm. thick, obscurely ribbed, dividing at the top into two very short basal arms. Basal arms bearing up to about 20 pinnae, pinna rachis about 3 mm. thick and up to 50 cm. long, rounded in section and bearing the pinnae laterally. Upper surface nearly smooth, lower bearing hairs. Hairs slender, simple, 0.5–1.0 mm. long, pointing backwards or outwards, composed of 3–5 cells; smaller hairs occurring in midribs and main veins. Most pinnules arising at right angles to the rachis but at about 70° near the free end. Pinnules typically 5 mm. wide (extremes 2–7 mm.) usually separated by gaps of 1 mm., rarely in contact. Pinnules becoming shorter and broader near the base of the leaf and finally forming marginal flanges with lobes about 1 mm. long and 1 cm. wide. Pinnules longest in middle region of pinna, typically 3–4 cm. (up to 6 cm. long); pinnules shorter and becoming triangular near apex of pinna. Adjacent pinnules connected by a web typically 2–3 mm. wide. Apices of pinnules obtusely pointed, margins entire, flat in sterile pinnules, slightly recurved in fertile pinnules. Surface of sterile pinnules flat. Surface of fertile pinnules flat or very slightly raised over each sorus. Substance of lamina delicate, veins projecting on lower side.

Midrib of pinnule very prominent, giving off laterals forking at once into forward and backward branches, which join those of adjacent veins to form primary arches. Primary arches usually wider than high, angular, never including any branch veins. Primary arches giving off 2–5 outer veins running nearly transversely to the margins and there bending slightly forward to join the marginal vein. Outer veins simple or branched, sometimes (especially in wide pinnae) anastomosing with adjacent branches to form elongated meshes. Basal web connecting adjacent pinnae containing strong forward and backward running veins close to the pinna rachis and giving off numerous outer branches which converge on the bay between adjacent pinnules. Venation in fertile pinnules as in sterile; placenta normally formed as a thickening of the top of the primary arch but occasionally on an outer branch vein just above the primary arch.

Placenta only slightly prominent but bearing the stumps of sporangia after maturity. Sporangia about 800 μ long, typically crowded in a regular ring of about 14. Spores rounded-tetrahedral, 34 μ wide (σ 3.5 μ), walls smooth, not very thick, triradiate cracks about 75 per cent of the spore radius, with conspicuously thickened borders. Epidermal cells of both sides of lamina with sinuous walls. Stomata oval, 30 μ wide scattered on lower surface, absent above.

DISTRIBUTION. *Phlebopteris polypodioides* is known only from the Middle Deltaic, and good specimens are confined to the Gristhorpe Bed. The other localities provided a few small fragments only.

Gristhorpe Series:

Gristhorpe Bed

Cloughton Wyke, *Neocalamites* Bed, Fern Bed.

Farndale Low Quarter Coalpits.

Harland Moor, Rose Cottage Coalpits.

Sycarham Series:

Beast Cliff, Bed A.

World Range. *P. polypodioides* is widespread from the Rhaetic to the Middle Jurassic in Europe. Outside Europe, it is rarer but occurs in E. Greenland (Rhaetic) and in Korea (Lower Jurassic) and there are a few more doubtful records. There are no well-authenticated specimens from the Upper Jurassic or Cretaceous.

DISCUSSION. While working on this material it became obvious that not only was the naming of certain Museum specimens confused, but my own earlier determinations based on general appearance often proved wrong. I have therefore limited myself to accepting only such specimens as show their characteristic venation: thus limited *P. polypodioides* proves rather constant apart from some variation in size of pinnules. All the previously figured specimens are probably from the Gristhorpe Bed and over half are fertile, though many show merely the denuded placenta (appearing as in Brongniart's figure). Often too the plane of cleavage cuts out each sorus leaving a neat hole in the lamina (cf. Lindley & Hutton, 1833, pl. 60). Specimens with a complete ring of sporangia still retain their spores and after discharge no sporangia, or only an occasional one remains attached to the placenta.

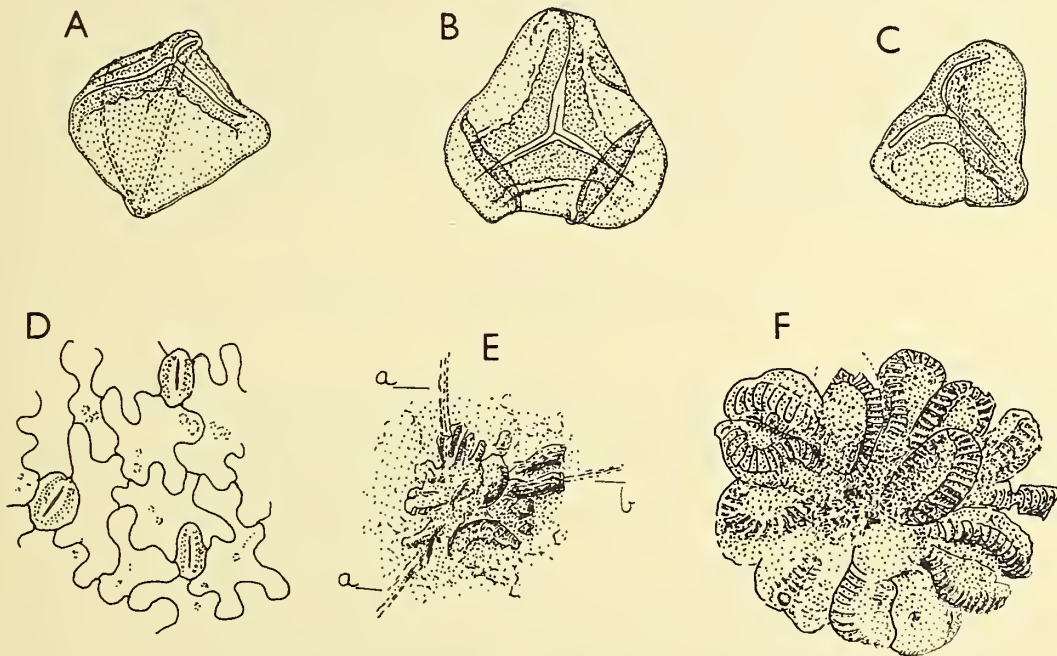


Fig. 34. *Phlebopteris polypodioides* Brongniart

A–C, spores. Leckenby Coll., 131, Sedgwick Museum, Cambridge, $\times 800$. D, lower epidermis, celloidin transfer, V.31950, $\times 200$. E, denuded placenta, 'a' is part of the primary vein arch (midrib to the left); 'b' the first outward vein branch. Celloidin transfer, V.31951, $\times 25$. F, sorus. Leckenby Coll., 131, Sedgwick Museum, Cambridge, $\times 25$. The leaf providing A–C, F is not the same as the one in Text-fig. 33 B, C.

A–C, F, imperfectly localised. D, E, Gristhorpe Bed.

No cuticle is preserved, but some of the Gristhorpe specimens had undergone a natural maceration and the lamina is reduced to an epidermal film which sometimes shows stomata very clearly. It is from such specimens that the fungal fructifications described earlier were obtained.

Phillips' *Pecopteris crenifolia* and Lindley & Hutton's *P. propinqua* are included in this species in spite of their crenate margins. Fertile specimens with bulging sori sometimes show a little matrix between the sori, thus giving apparent crenulations which disappear when the specimen is cleaned. Lindley & Hutton's *Pecopteris polypodioides* is also included as I believe

their figure of the venation is wrong. The rather similar venation seen in Seward (1900, text-fig. 10) is incomplete, the sori are all situated on typical vein arches. In all the specimens figured by Seward (1900, pls. 12, 13) the venation is normal. The earliest name is *P. caespitosa* Phillips (1829) but I have refrained from making a change.

COMPARISON. *Phlebopteris polypodioides* is distinguished from all other species by its primary vein arches which bear the sorus. The hairs may be somewhat characteristic but it is known that similar or larger ones occur in the Indian *P. hirsuta* Sahni & Sitholey (1945). In the absence of clear venation I have refrained from identifying Yorkshire specimens, and naturally I have also been reluctant to accept identifications of others where the veins are not shown.

In agreement with Hirmer & Hoerhammer (1936) *P. affinis* of the older Jurassic is here united with *P. polypodioides*. There may, however, be a slight difference in range of form. From the photographs of Hirmer & Hoerhammer (not their diagrammatic text-figure) it appears that about one tenth of the lateral veins converge before the margin to form loops. In Yorkshire specimens the proportion is higher, and in the widest pinnules second meshes are formed, a state unknown in the Rhaetic or Lower Liassic. It seems too that the primary arches are often flatter in the older specimens.

Phlebopteris woodwardi Leckenby

Text-fig. 35

1. Yorkshire specimens.

- 1864 *Phlebopteris woodwardi* Leckenby, p. 81, pl. 8, fig. 6. (Small fertile fragment, venation.)
- 1875 *Phlebopteris phillipsi* Phillips, p. 202, lign. 11 A, B. (Fertile pinnule, venation.)
- 1899 *Laccopteris woodwardi* (Leckenby) Seward, p. 198, text-fig. 9 A. (Venation of fertile pinnule, distinction from *P. polypodioides* doubted.)
- 1900 *Laccopteris woodwardi* (Leckenby): Seward, p. 84, text-fig. 11 A. (As Seward, 1899.)

2. Specimens from other regions.

- ?1859 *Carolopteris aquensis* Debey & Ettingshausen, p. 286, pl. 3, figs. 20-27. (Sterile and fertile pinnules, veins. Lower Cretaceous; Germany.)
- 1873 *Microdictyon woodwardianum* Saporta, p. 313, pl. 33, figs. 5-7. (Sterile and fertile fragments. Bathonian; France.)
- 1892 *Microdictyon* smlgn. *woodwardianum* Sap.: Bartholin, p. 24, pl. 10, figs. 2-4a. (Fertile pinnae, veins. Lower Lias; Bornholm.)
- 1899 *Laccopteris*, Seward, p. 198, text-fig. 11 C. (Fertile fragment. Inferior Oolite; English Midlands.)
- 1900 *Laccopteris*, Seward, p. 85, text-fig. 11 C. (As Seward, 1899.)
- 1904 *Laccopteris woodwardi* (Leckenby): Seward, p. 87. (Brief discussion.)
- 1910 *Laccopteris*, Seward, p. 359, text-fig. 267 C. (As Seward, 1899.)
- 1913 *Laccopteris* sp. 1, Möller & Halle, p. 24, pl. 3, figs. 13-17. (Small fragments. Lower Cretaceous; S. Sweden.)
- 1913 *Phlebopteris woodwardi* Leckenby: Lignier, p. 73, pl. 9, fig. 16; text-fig. 2. (Fertile fragment. Inferior Oolite; N. France.)
- ?1927 *Laccopteris rigida* Carpentier, p. 25, pl. 3, figs. 3-5, ?6, ?7; text-fig. 8. (Sterile and fertile pinnae. Wealden; N. France, or possibly = *P. dunkeri*.)
- 1927 *Laccopteris* Hirmer, p. 630, text-fig. 762 C. (As Seward, 1899.)
- ?1929 *Laccopteris woodwardi* (Leckenby): Edwards, p. 390. (Inferior Oolite; Sardinia.)
- ?1957 *Phlebopteris* sp., Stanislavski, p. 29, text-fig. 4. (S. Russia.)

EMENDED DIAGNOSIS. (Leaf as a whole unknown.) Pinnules linear, arising at right angles to the pinna rachis, width typically 5-6 mm. (rarely up to 10 mm.) near the base, tapering to about 3 mm. near the apex, apex blunt; length exceeding 4 cm. (estimated at about 6 cm.).

Adjacent pinnules separated by gaps of up to about 2 mm., connected by a web of lamina along the pinna rachis. Margins of pinnules entire, often recurved in fertile pinnules. Substance of lamina very thick, veins usually projecting below but flush above. Midrib broad and very prominent below, narrow and slightly prominent above. Surface of sterile lamina nearly flat but surface in fertile pinnule usually raised to form a hemispherical bulge above each sorus.

VENATION. Midrib bearing laterals at intervals of about 1 mm.; laterals forking at once into forward and backward branches. In sterile pinnules both branches forking once or twice more and all branches diverging; forward branches of one system usually uniting with a backward branch of the next, to form a rather high arch but sometimes no union occurring and all branches reaching the margin. Primary arches rarely low and then only in pinnules where frequent secondary anastomoses occur. Occasionally, frequent branching and anastomosis occurring to form elongated meshes. In fertile parts of pinnules, main vein branches arching round the soral bulge and usually (but not always) forming a high arch. Arch giving off about four parallel veins which run to the margin usually without further branching, but occasionally with branching and anastomosis. Sorus supplied by a short forward running vein branch from near the midrib, no other veins occurring inside primary arch. (Venation of basal web not known.)

Placenta very prominent, expanding apically, apical expansion sometimes lost after the sporangia have fallen off. Sporangia about 45μ long, in a ring of about 6 (5-8). (Spores not observed.)

Epidermal cells probably polygonal with strongly raised anticlinal walls. Midrib without hairs.

DISTRIBUTION. *Phlebopteris woodwardi* is commonest in the Lower Deltaic but occurs throughout the whole Series as follows:

Upper Deltaic: South Cliff, Scarborough.

Scalby Wyke, level bedded series.

Middle Deltaic, Gristhorpe Series:

Above the Gristhorpe Bed (abundant).

Cloughton Wyke, *Solenites* Bed; *quinqueloba* Bed.

Riccal Dale Coalpits.

Jugger Howe, Helwath.

Lower Deltaic: Hawsker, Jack Ass Trod *Nilssonina* Bed.

Hawsker, Gnipe Howe, Maw Hole fallen block.

Haiburn, just below Iron Scar.

Beast Cliff, fallen blocks at many points in matrix like that of Haiburn, below Iron Scar.

Haiburn Wyke *Zamites* Bed.

Ravenscar, Peak Alum pit.

Ravenscar, Brow Alum pit.

Ravenscar, Fox cliff.

Ingleby Arncliffe, Cop Loaf Quarry.

Farndale, Hillhouse Nab plant bed.

Rosedale, Hartoft Coalpit.

World Range. Fragments agreeing with *P. woodwardi* are confined to Europe and range from the Liassic (Bornholm) to the Lower Cretaceous of Sweden, Germany and N. France.

DISCUSSION. In Yorkshire, *P. woodwardi* is represented by an enormous number of small fragments and no large pieces at all. At several localities bedding planes are covered with

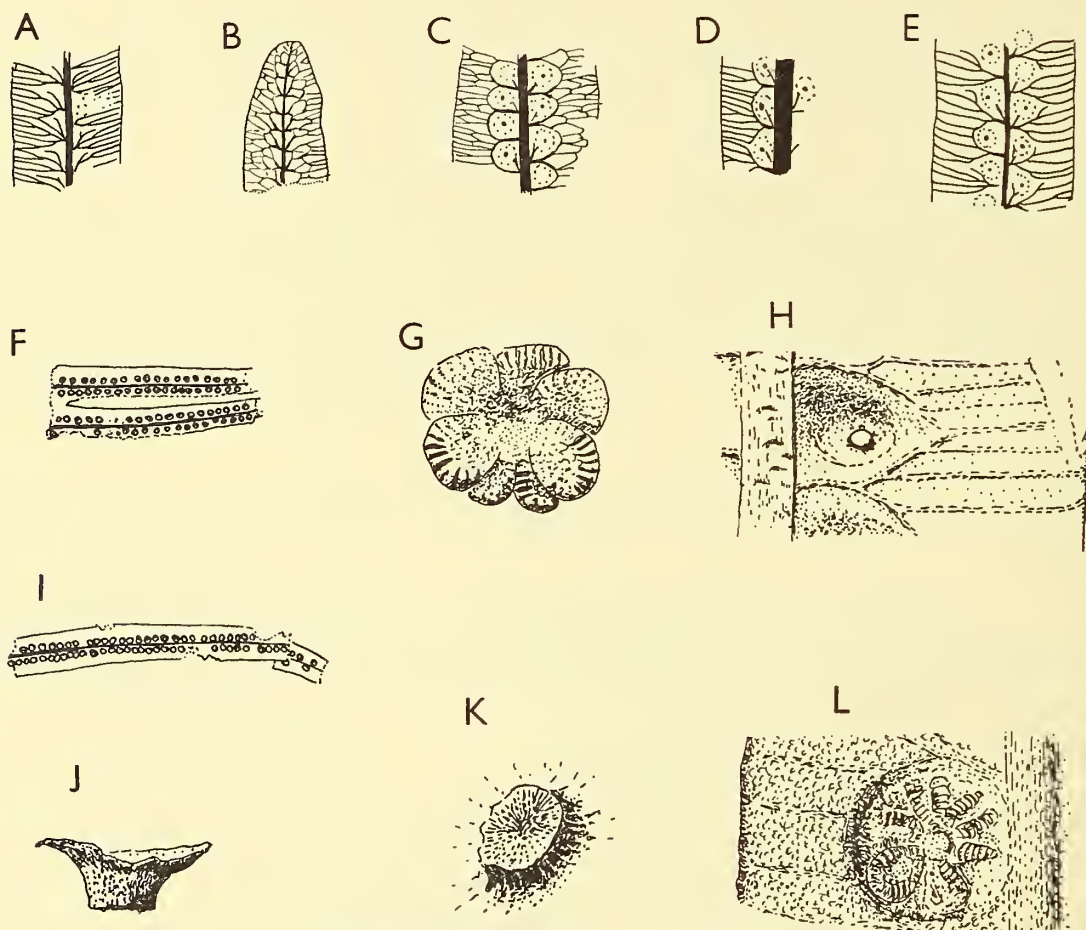


Fig. 35. *Phlebopteris woodwardi* Leckenby

A-E, typical fragments, V.28506, $\times 3$. In A some of the veins are obscure and have been omitted. F, two pinnules in balsam transfer; the margins are recurved, making the pinnules appear too narrow, V.31959, $\times 1$. G, one sorus from F, $\times 25$. Here the placenta is slightly sunken. H, fertile pinnule which has shed its sporangia, in balsam transfer, V.31954, $\times 10$. I, Fertile pinnule, V.31953, $\times 1$. J, displaced placenta from the same preparation as H, $\times 40$. K, placenta of H, $\times 40$. L, sorus with slightly raised placenta, $\times 25$. (Specimen lost in further preparation.) A-E, above Gristhorpe Bed. F, G, Hawsker Jack Ass Trod *Nilsson* Bed. H-K, Roseberry Topping.

pinnule fragments of this species and often occur with no other determinable fossil. The preservation is remarkable for the fragments are preserved not as coaly compressions but as unconsolidated charcoal (fusain) in which the separate cells can be seen; many for example have split in the plane of the veins separating the palisade from the spongy mesophyll, the cells of both of which are to be seen.

This preservation is peculiar to *P. woodwardi*; no other leaf is chiefly preserved as charcoal but great numbers of wood fragments are so preserved. (A few associated bits of *Matonidium* are similar.) It is certainly not caused by the treatment which the sediment has undergone (for in several localities other associated leaves are preserved in the ordinary way). It may have been caused by burning and the pinnule fragments may represent small pieces of true charcoal resulting from widespread fires. I imagine *P. woodwardi* an abundant plant of inland heaths from which plant material would seldom be preserved in the delta except as a result of burning and then flood.

This species is one which Hirmer & Hoerhammer (1936) transferred to *Nathorstia*, but without discussion. The sorus, however, looks like that of other species of *Phlebopteris* except that it is small and there are fewer sporangia. The same slight irregularity in sporangial orientation is to be seen and occasionally a sporangium is considerably displaced, proving it to be separate from its neighbours. After spore discharge, the sporangia fall off leaving the placenta bare. The placenta is only well seen in transfers as the upper side of the pinnule is usually exposed. Even in transfers the top of the placenta is sometimes missing, probably as a result of abrasion before preservation. When complete it is very like the reconstruction of *Matonidium* given by Hirmer & Hoerhammer (1936) and this raises the question of the correct genus for *P. woodwardi*. This question is left until more species are examined by balsam transfers.

Further work. The Lower Cretaceous specimens called *Carolopteris aquensis* should be re-examined, for the name *aquensis* may well prove valid of this species.

The Yorkshire material offers no promise of advance in understanding this little known species, since it is so thoroughly broken, nor is there any prospect of preparing spores from the charred sporangia, but floras, e.g. at Bornholm, providing more complete specimens offer a better chance for progress.

COMPARISON. *Phlebopteris woodwardi* was only vaguely distinguished from *P. polypodioides* by Seward (1900) and later (1904) the distinction was doubted. *P. woodwardi* is, however, sharply distinguished by the dome over its sorus which is inside and not on the primary vein mesh. The sorus is nearer the midrib and the substance of the lamina is much thicker. The character used by Seward, the more frequent vein anastomosis is unreliable for about three fourths of the fragments of *P. woodwardi* show few or none. It is true, however, that some show them in great numbers.

P. woodwardi is closer to *P. dunkeri* and some of the figures could equally well represent either. A difference is that the sorus is always close to the midrib in *P. woodwardi* but a little farther out in *P. dunkeri* and it is on these grounds that Raciborski's specimens might be included in *P. dunkeri*. Where the fine venation is visible the numerous small veins inside in the primary arch of *P. dunkeri* serve to distinguish it clearly.

Phlebopteris dunkeri (Schenk) Schenk

Text-fig. 36 A-C

None of the following is from Yorkshire.

- 1871 *Laccopteris dunkeri* Schenk, p. 219, figs. 3-5. (Fragments rather like *Phlebopteris woodwardi*. Wealden; N. Germany.)
- 1872 *Microdictyon rutenicum* Saporta, p. 309, pl. 33, figs. 2-4; pl. 35, fig. 3. (Sterile and fertile fragments. Bathonian; France.)

- 1875 *Microdictyon dunkeri* (Schenk) Schenk, p. 161, pl. 27, fig. 10; pl. 28, fig. 11a-d. Named *Phlebopteris dunkeri* on plates. (Good figures of venation and details of sorus. Lower Cretaceous; Germany.)
- 1880 *Laccopteris dunkeri* Schenk: Hosius & Von der Marck, p. 208, pl. 44, figs. 192, 193. (Sketch of fertile pinnules. Lower Cretaceous; Germany.)
- 1888 *Laccopteris dunkeri* Schenk: Velenovsky, p. 12, pl. 2, figs. 3-7. (Fertile pinnae, veins. Cretaceous; Bohemia.)
- 1894 *Microdictyon woodwardianum* Sap.: Raciborski, p. 184, pl. 13, figs. 10-14. (Venation of fertile pinnule, sorus. Upper Lias; Poland.)
- 1894 *Microdictyon dunkeri* (Schenk): Seward, p. 135. (Record from English Wealden.)
- ?1899 *Drynaria astrostigma* Bayer, p. 9, pl. 1, figs. 5, 6; text-fig. 4. (Sterile and fertile pinnules, venation shown schematically. Bohemia.)
- ?1899 *Drynaria fascia* Bayer, p. 10, text-fig. 5.
- ?1899 *Drynaria dura* (Velen.) Bayer, p. 15, text-fig. 6.
- ?1899 *Drynaria tumulosa* Bayer, p. 19, pl. 1, figs. 1-4.
- ?1901 *Drynaria astrostigma*, *D. fascia*, etc.: Fric & Bayer, pp. 70-73, text-figs. 7-10. (As Bayer, 1899 and Velenovsky, 1888.)
- 1911a *Laccopteris dunkeri* Schenk: Seward, p. 661, pl. 1, figs. 5-13; pl. 5, fig. 101, 101A; pl. 6, fig. 7; text-fig. 4. (Fragments. Upper Oolite; Scotland.)
- 1913 *Laccopteris* ? sp. 2, Möller & Halle, p. 26, pl. 3, figs. 18-20. (Sterile fragments. Lower Cretaceous; Sweden.)
- 1920 *Drynaria tumulosa* Bayer: Bayer, p. 9, text-fig. 2. (Bohemia.)
- 1927 *Laccopteris rigida* Carpentier, p. 25, pl. 3, figs. 3-5, ?6, ?7; text-fig. 8. (Sterile and fertile fragments equally like *P. woodwardi*. Wealden; N. France.)
- 1933 *Laccopteris dunkeri* var. *longipennis* Kryshstofovich, pl. 4, figs. 3-5. (Good sterile and fertile specimens. Lower Cretaceous; Siberia.)
- ?1957 *Laccopteris dunkeri* Schenk: Semaka, p. 335, text-figs. 24, 25. (Fertile leaf, possibly *P. polypodioides*. Lias; Roumania.)

This synonymy makes no attempt to deal with Upper Cretaceous specimens usually included in *Nathorstia*.

EMENDED DIAGNOSIS. (Leaf as a whole not known.) Pinnae long with a rachis up to 3 mm. wide. Pinnules linear, arising almost at right angles to the rachis; width typically 6-9 mm. at the base, tapering toward the blunt apex, length exceeding 5 cm. Adjacent pinnules separated by gaps up to 2 mm. wide, lamina connected by a broad web along the pinna rachis. Substance of lamina not very thick. Midrib prominent below; main veins arising at intervals of about 1 mm. and forking at about midway between the midrib and margin. In sterile pinnules area of main arches occupied by several small veins arising from the midrib and sides and top of the arch; outer part of lamina also occupied by small veins passing from the top of the arch to the marginal vein, small veins branching and anastomosing to form numerous minute isodiametric or slightly elongated meshes. In fertile pinnules, sori forming conspicuous bulges on the upper surface, situated at some distance from the midrib, in the centre of the primary arches and supplied by several convergent veins. Fine vein network similar to sterile pinna. Sporangia 6-12, about 700 μ long. Spores rounded tetrahedral, size unknown.

This diagnosis is based largely on the figures of Schenk (1875), Raciborski (1894) and Kryshstofovich (1933).

DISTRIBUTION. *Phlebopteris dunkeri* is a rare species of the Yorkshire Lower Deltaic; the only specimen was found in the Lower Deltaic Plant bed near Petard Point, Beast Cliff just above the High Water mark. Elsewhere it occurs in rocks of about the same age in France and Poland. It occurs in the Upper Jurassic of Scotland but only becomes frequent in the Lower Cretaceous of Europe. Its range in the Cretaceous is at present obscure because of confusion with similar looking ferns included in *Nathorstia*.

DISCUSSION. The only Yorkshire specimen was a tiny piece of shale bearing an ill-preserved fragment on one side and a larger but indistinct imprint on the other. The small fragment was transferred with the sacrifice of the larger imprint. The figures show all the recognisable features, and these agree with *P. dunkeri* alone among Mesozoic plants.

The lamina is translucent and shows scattered dark spots suggestive of stomata but no epidermal cells were seen.

COMPARISON. *P. dunkeri* resembles *P. woodwardi* (see p. 106) but is distinguished by the details of venation and the precise position of the sorus. Its relation to several species of Cretaceous ferns placed in *Nathorstia* needs investigation.

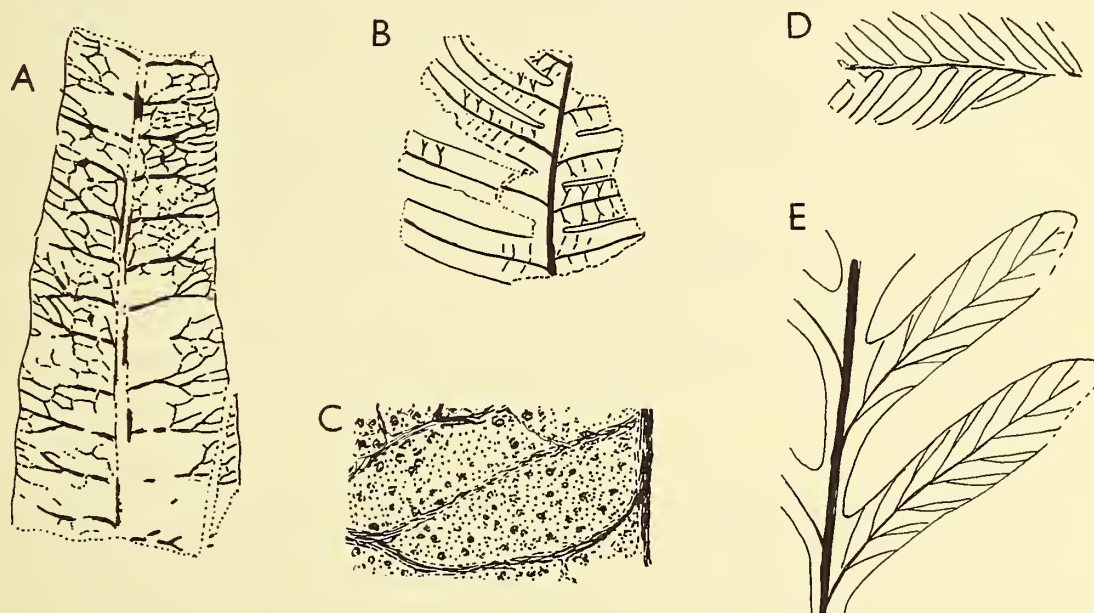


Fig. 36. *Phlebopteris dunkeri* (Schenk); *Selenocarpus muensterianus* (Presl)

A-C, *P. dunkeri*. A, pinnule fragment in balsam transfer, V.31949, $\times 5$. B, imprint of part of pinna on the same piece of shale as A, $\times 1$. C, details of part of A showing veins ending in the marginal rib and the granules (? stomata) in the lamina, $\times 40$.

D, E, *S. muensterianus*. D, sterile pinna fragment, V.32100, $\times 1$. E, part of D, $\times 4$.

A-C, Beast Cliff. D, E, Hasty Bank.

Genus SELENOCARPUS Schenk, 1867:89

This genus differs from *Phlebopteris* only in its sorus which is semicircular instead of being round. *S. muensterianus* is the only species.

Selenocarpus muensterianus (Presl) Schenk

Text-fig. 36 D, E

All of the following are from Germany.

- 1838 *Taxodites muensterianus* Presl in Sternberg, p. 204, pl. 33, fig. 3.
- 1852 *Thinnfeldia muensteriana* (Presl) Ettingshausen, p. 5, pl. 2, figs. 1, 2.
- 1852 *Thinnfeldia parvifolia* Ettingshausen, p. 6, pl. 2, fig. 3.
- 1867 *Selenocarpus muensterianus* (Presl) Schenk, p. 89, pl. 22, figs. 1, 2, 5, 6.
- 1869 *Selenocarpus muensterianus* (Presl): Schimper, p. 575, pl. 39, figs. 1-3. (Figures from Schenk, 1867.)

- 1914 *Selenocarpus muensterianus* (Presl): Gothan, p. 15, pl. 17, figs. 1, 2; text-fig. 2. (Sterile and fertile fragments, sporangia.)
 1936 *Selenocarpus muensterianus* (Presl): Hirmer & Hoerhammer p. 38, pls. 8, 9; pl. 10, figs. 1-3; text-fig. 5:5. (Good sterile and fertile leaves, sporangia, spores; full literature.)

EMENDED DIAGNOSIS (based on German material). Petiole about 2 mm. wide, smooth, dividing at the top into two very short basal arms bearing 7-15 pinnae. Pinna up to about 20 cm. long, typically about 15 mm. wide, bearing pinnules at intervals of about 5 mm. Pinnules linear arising at an angle of 45° , apex obtuse, margins entire; width 1-2 mm., slightly narrowed near the base, basal margin decurrent as a narrow wing along the pinna rachis.

VENATION. Midrib arising at a small angle near the base of the pinnule and bending outwards. Lateral veins arising in katadromic order or nearly opposite, simple or once forked, never anastomosing, arising at intervals of 1-3 mm. and at an angle of about 40° . Substance of lamina fairly thick, margins flat.

Fertile leaf similar to sterile, sori borne one on each main lateral vein. Sorus without indusium, consisting of a placenta bearing a semicircle of sporangia, the concavity facing outwards. Sporangia about 0.5 mm. wide, annulus prominent, probably complete and oblique. Spores numerous, rounded triangular about 34μ - 47μ wide; wall fairly thick, smooth; tri-radiate scar well developed probably with a conspicuous margin.

DISTRIBUTION. All the previously known specimens are from the Lower Lias of S.W. Germany (Franconia) where the species is frequent. The Yorkshire specimens (which thus add to its range) are from the base of the Lower Deltaic Series, from Hasty Bank and Esklets Cragg, Westerdale.

DISCUSSION. *S. muensterianus* is represented in Yorkshire by a few fragments of sterile pinnae, the best being figured here. It agrees with the German specimens in size and in the very characteristic pinnules which arise at an unusually small angle, narrow below and have a decurrent basal margin. The veins arise at a remarkably small angle. No other fossil fern known to me shares these characters so that the specimen is determined with some confidence even in the absence of fertile material.

Genus MATONIDIUM Schenk, 1871:219

The only character distinguishing this genus from *Phlebopteris* is the expanded end of the placenta which forms an indusium, and as shown above *P. woodwardi* closely approaches *Matonidium*. It is usually held that the series *Phlebopteris*-*Matonidium*-*Matonia* represents progressive evolution.

TYPE SPECIES. *Matonidium goepperti* (Ettingshausen).

Matonidium goepperti (Ettingshausen) Schenk

Text-figs. 37, 38

1. Yorkshire specimens.

- 1864 *Pecopteris polydactyla* Dunker: Leckenby, p. 80, pl. 11, fig. 1, 1a. (Good leaf.)
 1875 *Pecopteris caespitosa* Phillips, p. 207 (in part), lign. 20. (Typical pinna. Pl. 8, fig. 10 is *Phlebopteris polydactyloides*.)
 1900 *Matonidium goepperti* (Ettings.): Seward, p. 74, pl. 11, figs. 1-3; text-fig. 7 A (? not B). (Good fertile leaves.)
 1910 *Matonidium goepperti* (Ettings.): Seward, p. 362, text-fig. 269. (Reduced from Seward, 1900, pl. 11.)
 1911b *Matonidium goepperti* (Ettings.): Seward, p. 5, text-fig. 2 (as Seward, 1910).
 1927 *Matonidium goepperti* (Ettings.): Hirmer, p. 633, text-figs. 765-766. (Copies of Seward, 1900, pl. 11.)

2. Specimens from other regions.

- 1846 *Pecopteris althausi* Dunker, p. 5, pl. 2, fig. 2. (Sterile pinna. Wealden; N. Germany.)
 1846 *Pecopteris polydactyla* Dunker, p. 5, pl. 7, fig. 4. (Sterile pinna. Wealden; N. Germany.)
 1846 *Pecopteris conybeari* Dunker, p. 5, pl. 9, fig. 8, 8a. (Small leaf base. Wealden; N. Germany.)
 1846 *Alethopteris elegans* Dunker, p. 8, pl. 7, fig. 7. (Sterile pinnae. Wealden; N. Germany.)
 1852 *Alethopteris goepperti* Ettingshausen, p. 16, pl. 5, figs. 1-7. (Good specimens. Cretaceous; Germany.)
 1869 *Laccopteris goepperti* (Ettings.) Schimper, p. 582, pl. 31, figs. 5-8. (Copies from Dunker, 1846, pl. 7, fig. 7; pl. 9, fig. 8.)
 1869 *Laccopteris Phillipsii* Zigno: Schimper, p. 582, pl. 31, fig. 9. (Copy from Dunker, 1846, pl. 7, fig. 4.)
 1870 *Pecopteris althausi* Dunker: Trautschold, p. 216, pl. 19, fig. 3. (Fertile pinna. Cretaceous; Russia.)
 1870 *Pecopteris psychycarpa* Trautschold, p. 218, pl. 19, fig. 6. (Fertile pinna.)
 1870 *Pecopteris explanata* Trautschold, p. 226, pl. 19, fig. 7. (Fertile pinna.)
 1871 *Matonidium goepperti* (Ettings.) Schenk, p. 219, pl. 27, fig. 5; pl. 28, figs. 1, 2; pl. 30, fig. 3; pl. 42, fig. 1. (Good sterile and fertile leaves, venation. Wealden; Germany.)
 1875 *Matonidium goepperti* (Ettings.): Schenk, p. 160, pl. 27, fig. 9. (Wealden; Germany.)
 1881 *Matonidium goepperti* (Ettings.): Heer, p. 16, pl. 15, figs. 1-6. (Cretaceous; Portugal.)
 1894 *Matonidium goepperti* (Ettings.): Saprota, p. 104, pl. 19, fig. 5. (See Teixeira, 1948: 38.)
 1894 *Matonidium goepperti* (Ettings.): Seward, p. 63, text-figs. 7, 8. (Fertile pinnae. Wealden; S. England.)
 1899 *Matonidium althausi* (Dunker) Ward, p. 653. (Revival of older specific name.)
 1900a *Matonidium goepperti* (Ettings.): Seward, p. 10, pl. 1, figs. 1, 2. (Sterile fragments. Wealden; Belgium.)
 1905 *Matonidium althausi* (Dunker): Fontaine in Ward, p. 230. (Name; ? not fig.)
 1911a *Matonidium goepperti* (Ettings.): Seward, p. 662, pl. 2, figs. 25, 26. (Sterile pinna. Upper Jurassic; Scotland.)
 1913 *Laccopteris rotzoana* Zigno: Grandori, p. 81, pl. 6, fig. 23. (Upper Lias; Italy.)
 1913 *Matonidium goepperti* (Ettings.): Seward, p. 89, pl. 14, fig. 3a. (Pinna. Lower Cretaceous; England.)
 1923 *Matonidium* cf. *goepperti* (Ettings.): Lipps, p. 332, text-figs. 1-3. (Germany.)
 1936 *Matonidium goepperti* (Ettings.): Hirmer & Hoerhammer, p. 42, pl. 10, figs. 4-6; text-figs. 5, 6, 6d. (Good fertile pinna, sorus, spores. Wealden; N. Germany.)
 1948 *Matonidium goepperti* (Ettings.): Teixeira, p. 33, pl. 15, figs. 1-6; pl. 16, figs. 1-4. (Good leaves. Cretaceous; Portugal.) Also possibly on pp. 38, 40, 46, 49, 92, 93; pl. 13, fig. 5; pl. 43, fig. 5, pinna fragments.
 1952 *Matonidium goepperti* (Ettings.): Teixeira, p. 135, pl. 7, figs. 3-5. (Portugal.)

The following are distinct:

- 1829 *Pecopteris caespitosa* Phillips, p. 148, pl. 8, fig. 10. (Yorkshire specimen identified with *Matonidium* by Hirmer & Hoerhammer, 1936, p. 42.)
 1927 *Matonidium goepperti* (Ettings.): Yabe, p. 51. (Renamed *Cladophlebis matonioides* by Oishi, 1940: 158, 274.)
 1923 *Matonidium* oder *Laccopteris*, Gothan, p. 775, text-figs. 4, 5. (Pinnules broader and lobed. Germany.)

EMENDED DIAGNOSIS. Petiole about 5 mm. thick, straight, slightly striated longitudinally; dividing apically into two short basal arms. Basal arms bearing numerous (20 or more) pinnae. Pinnae very slender, typically about 20 cm. long, rachis about 1 mm. and total width with pinnules about 1.5 cm.; largest pinnae with a rachis 2 mm. thick and pinnules 2.5 cm. long. Pinna rachis smooth, projecting more below than above, hairless.

Pinnules typically 1 mm. broad, slightly wider at the base and narrowing towards the apex. Length in middle region of pinna about 7.5 mm., shape rather falcate. Basal pinnules very short but 1 mm. broad and distinct; apical ones small and narrow. Adjacent pinnules connected by a web of lamina about 0.5 mm. wide. Margins of pinnules entire (sometimes very slightly lobed); often reflexed especially when fertile. Midrib conspicuous on under side.

Substance of lamina rather thick, veins often obscure. In smaller sterile pinnules lateral veins arising at a concentration of about 2 per mm., forking once and meeting the margin at an angle of 60°-70° and ending in a marginal rib. In larger sterile pinnules veins mostly forked twice. In fertile pinnules veins forked at their origin; forward branch supplying sorus, backward branch running at an angle of about 80° to the margin and usually forked just before the margin. Surface of lamina usually bulging above each sorus.

Basal web showing several veins converging on the margin (in small pinnules). (Possibly with an anastomosing vein alongside pinna rachis in large ones, but no other vein anastomosis occurring.)

Sori about 500μ wide typically rather crowded except near apex of fertile pinnule, situated midway between midrib and margin. Placenta prominent, ending in a persistent indusium about 0.25 mm. wide; margins of indusium membranous, not extending as far as the sporangia.

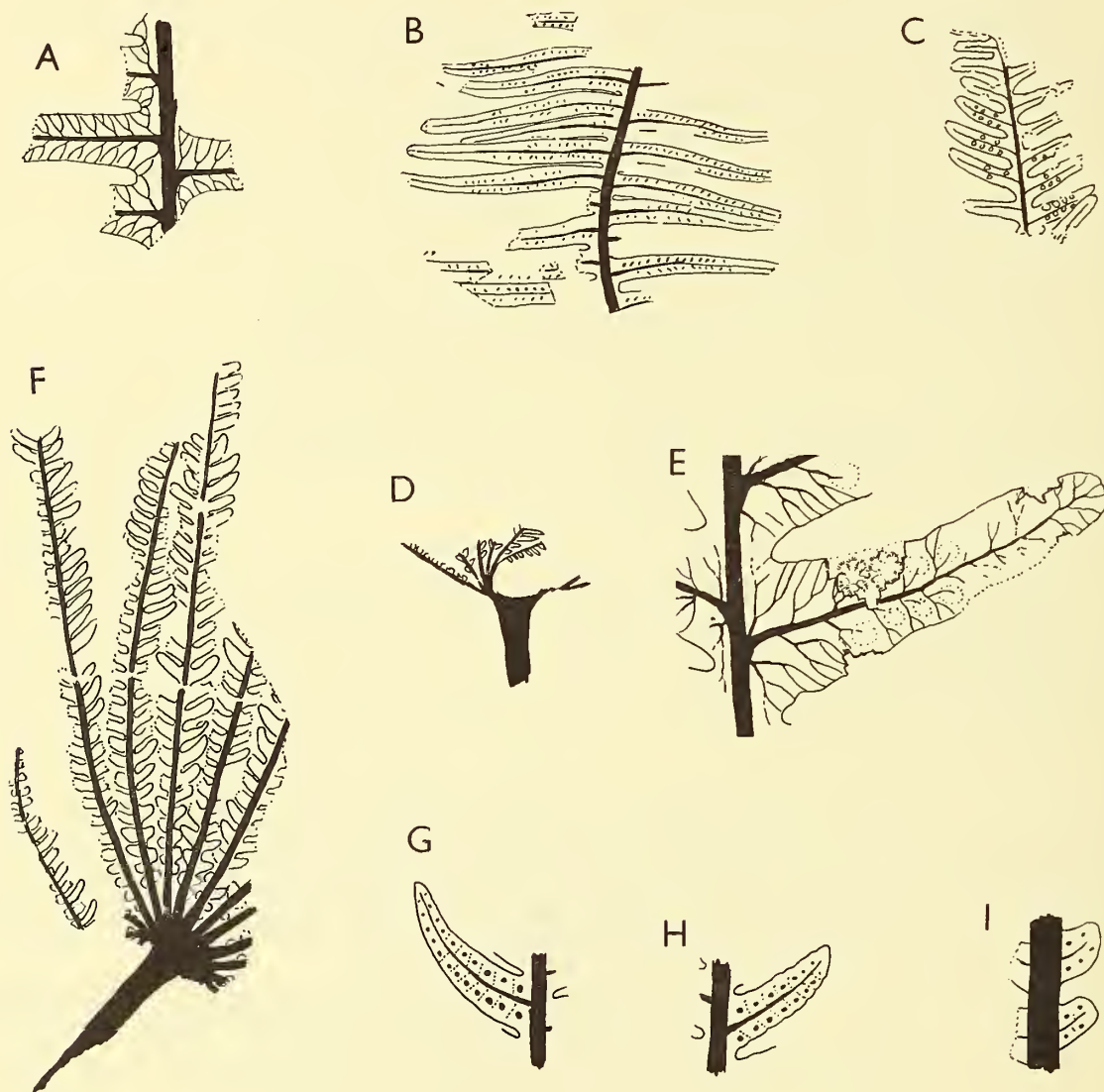


Fig. 37. *Matonidium goepperti* (Ettingshausen)

A, sterile fragment showing the venation, V.25229, $\times 4$. B, fragment of exceptionally large fertile pinna (apices of pinnules sterile), V.31920, $\times 1$. C, apex of large fertile pinna (see E for details), V.21481, $\times 1$. D, leaf base; the pinnae in the middle are immersed in the rock and the small pinnae are pointing upwards, V.31920, $\times 1$. E, lower pinnule from C showing veins and imprint of sporangia on the rock beneath, $\times 5$. F, base of fertile leaf, V.31921, $\times 1$. G, H, I, pinnules from different parts of F; the veins are mostly unseen, $\times 4$. A is from Gristhorpe (probably above the Gristhorpe Bed). B, C, E, Gristhorpe Bed. D, F-I, Haiburn *Zamites* Bed.

Sporangia forming a more or less regular ring of typically about 10; annulus very well developed.

Spores 44μ wide (σ 4μ), rounded-tetrahedral with rather thick smooth walls; triradiate cracks up to about three-quarters of the spore radius with broad and strongly thickened borders.

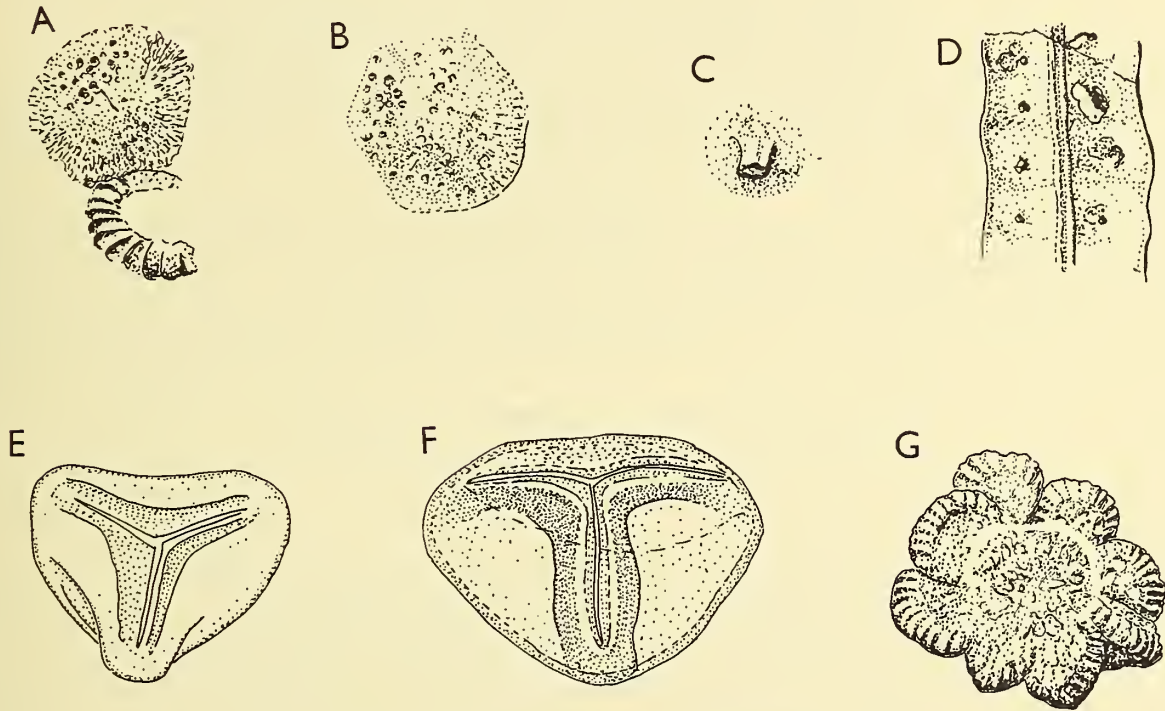


Fig. 38. *Matonidium goepperti* (Ettingshausen)

A, B, indusia of two neighbouring sori, as seen in transfer, V.31982a, $\times 40$. C, indusium of same specimen, as originally exposed showing the stalk but not the true margin, $\times 40$. D, pinnule in balsam transfer showing more or less broken indusia or their stalks, but only an occasional sporangial fragment, V.31982a, $\times 8$. E, rather small and thin-walled spore, V.31922, $\times 800$. F, normal spore, V.31982a, $\times 800$. G, sorus of V.31922 as seen in transfer, $\times 40$.

A–D, F, from Gristhorpe Bed. E, G, Saltwick *Matonidium* Bed.

DISTRIBUTION. *M. goepperti* is locally abundant in a layer of ironstone at Haiburn and all of the numerous Museum specimens seem to be from this bed. It is also abundant and well preserved in shales at several points in the Cliffs south of Whitby but these localities are only known from fallen blocks. The species is commonest in the Lower Deltaic. Its distribution in Yorkshire is as follows:

Middle Deltaic, Gristhorpe Series:

Gristhorpe Bed.

With *Phlebopteris woodwardi* at Gristhorpe; probably in the bed above the Gristhorpe Bed.

Middle Deltaic Sycarham Series:

Cloughton, 25 ft. above the Iron Scar.

Lower Deltaic:

Whitby, Rail Hole Bight, fallen blocks.
 Saltwick, *Matonidium* Bed, fallen blocks.
 Hawsker, Widdy Head, fallen blocks.
 Hawsker, Maw Wyke, fallen blocks.
 Hawsker, Jack Ass Trod, *Nilssonia* Bed. (Obscure fragment.)
 Haiburn *Zamites* Bed, especially in an ironstone layer.
 Ravenscar Brick Works, *Matonidium* Bed (fallen blocks).

Outside Yorkshire, *M. goepperti* is widespread in the European Upper Jurassic and Lower Cretaceous (the Yorkshire specimens are the oldest known). It is not yet known outside this region.

DISCUSSION. The numerous specimens agree well with one another but there is a tendency for the width of the pinnae to be greater in some localities than in others. For instance at Maw Wyke and at Widdy Head the average width of pinna is about 11 mm.; and at Haiburn it is only a little greater; at Saltwick the average is between 2 and 3 cm. and the widest known are at Gristhorpe where one pinna nearly 5 cm. wide occurs (there are only four associated specimens all rather large). The wider specimens look rather like narrow forms of *Phlebopteris poly-podioides* but the venation is different; the spores are larger and thicker walled and the indusium is present, though sometimes needing to be transferred to be seen. The spores of these large specimens and a small one (from Rail Hole Bight, Whitby) are identical but those from an intermediate sized form at Saltwick are rather small and thin walled, possibly ill-developed.

The sporangia usually disappear after dehiscence but sometimes bits of the annulus remain. The placenta is often preserved and where it is missing it is believed to be the result of abrasion before deposition; it is of course easily damaged in transferring. Where it is complete, it forms a peltate body with a rather slender stalk. The margin is a delicate membrane and much of it seems to be but a single cell thick. It is thus more extensive and less massive than is suggested by the diagram in Hirmer & Hoerhammer (1936: 45, text-fig. 6d).

The specific name *Matonidium goepperti* (Ettingshausen) is in general use and is here retained although the name *Pecopteris althausi* Dunker (1846) is older.

Family *DIPTERIDACEAE*

This family is poorly represented in the Yorkshire flora; two important genera, *Dictyophyllum* and *Clathropteris* make perhaps their last appearance and a third, *Hausmannia*, though in the middle of its range, is rare.

The Yorkshire species are separable from one another by the characters given below.

Pinnae deeply divided into lateral segments; vein meshes rarely rectangular; sporangia widespread.	<i>Dictyophyllum rugosum</i>
Pinnae only divided up to halfway to midrib; vein meshes tending to be rectangular; sori widely separated	<i>Clathropteris obovata</i>
Pinnae not divided laterally but forked longitudinally; vein meshes mostly rectangular; sori round but rather crowded	<i>Hausmannia dichotoma</i>

Genus *Dictyophyllum* Lindley & Hutton, 1834:65

In their useful review of the fossil Dipteridaceae, Oishi & Yamasita (1936) tried to define *Dictyophyllum* and *Thaumatopteris* more clearly and in doing so transferred *Dictyophyllum rugosum* to *Thaumatopteris*. The rule of priority, however, compels us to keep a type species in its original genus, whatever else has to be changed, and this species must retain its name. There is a case for using the specific name *D. nervulosum* (Phillips).

Thaumatopteris is a genus of insecure validity since the type species (*T. muensteri* Göppert) is regarded as a species of *Dictyophyllum* but it has come to be used for ferns resembling *T. schenki* and *T. brauni*. *Dictyophyllum rugosum* shares several characters with *T. schenki*—the short 'arms' of the leaf base; narrow, lobed lateral segments of the pinnae joined by a web of lamina at their bases and its fairly small sporangia. Its minute and crowded sori are, however, different and are like other kinds of *Dictyophyllum*.

There is no fundamental difference between *Dictyophyllum* and *Thaumatopteris* and if the name *Thaumatopteris* is to be retained it must be on the soral character alone. Ferns whose sori are unknown are best included in *Dictyophyllum*.

Dictyophyllum rugosum Lindley & Hutton

Text-figs. 39, 40, 41 D-I

1. Yorkshire specimens.

- 1829 *Phyllites nervulosus* Phillips (non Sternberg), p. 148, pl. 8, fig. 9. (Poor figure.)
- 1834 *Dictyophyllum rugosum* Lindley & Hutton, p. 65, pl. 104. (Good figure.)
- 1836 *Phlebopteris phillipsi* Brongniart, p. 377, pl. 132, fig. 3 (good figure), pl. 133, fig. 1. (Same figures as Phillips, 1829 and Lindley & Hutton, 1834.)
- 1856 *Dictyophyllum rugosum* L. & H.: Zigno, p. 176, pl. 23, fig. 2, 2a. (Good figure.)
- 1856 *Dictyophyllum leckenbyi* Zigno, p. 178, pl. 23, figs. 1, 1a. (Good figure.)
- 1875 *Phlebopteris phillipsi* Brongn.: Phillips, p. 202, lign. 11a, b, pl. 8, fig. 9. (Sketch of veins and figure as Phillips, 1829.)
- 1875 *Phlebopteris leckenbyi* (Zigno) Phillips, p. 203.
- 1900 *Dictyophyllum rugosum* L. & H.: Seward (in part), p. 122, pl. 13, fig. 3; text-fig. 19. (Other figures represent *Clathropteris obovata*.)
- 1922 *Dictyophyllum rugosum* L. & H.: Thomas, p. 110, pl. 1, figs. 1-4. (Good fertile fragments.)
- 1936 *Thaumatopteris rugosa* (L. & H.) Oishi & Yamasita, p. 152. (Change of name proposed.)
- 1944 *Dictyophyllum rugosum* L. & H.: Harris, p. 661, text-figs. 1-3.
- 1950 *Dictyophyllum rugosum* L. & H.: Harris, p. 1026, text-fig. 9 c.
- 1955 *Dictyophyllum rugosum* L. & H.: Couper, p. 471, pl. 20, figs. 6, 7. (Spores.)

2. Specimens from other regions.

- ?1906 *Dictyophyllum spectabile* Nathorst (in part), pl. 7, fig. 1 only. (Lower Lias; Germany.)
- ?1938 *Dictyophyllum rugosum* L. & H.: Prinada, p. 377, text-fig. 5. (Small fragments. Russia.)

The following are distinct:

- 1900 *Dictyophyllum rugosum* L. & H.: Seward, pl. 18, fig. 1; text-figs. 17, 18, ?19. (*Clathropteris obovata*; text-fig. 18 is repeated in Seward, 1910, text-fig. 283. Yorkshire.)
- 1917 *Dictyophyllum rugosum* L. & H.: Walkom, p. 9, pl. 4, fig. 8; pl. 6, fig. 4 B; pl. 9, fig. 3. (Queensland specimens renamed *D. bremerense* by Jones & de Jersey, 1947a.)
- 1924 *Dictyophyllum rugosum* L. & H.: Walkom, p. 82, pl. 21, fig. 1. (A distinct species of *Dictyophyllum*. Australia.)
- 1926 *Dictyophyllum rugosum* L. & H.: Moisseiev, p. 584, pl. 10, figs. 1-3, is not determinable from the figures. (Crimea.)

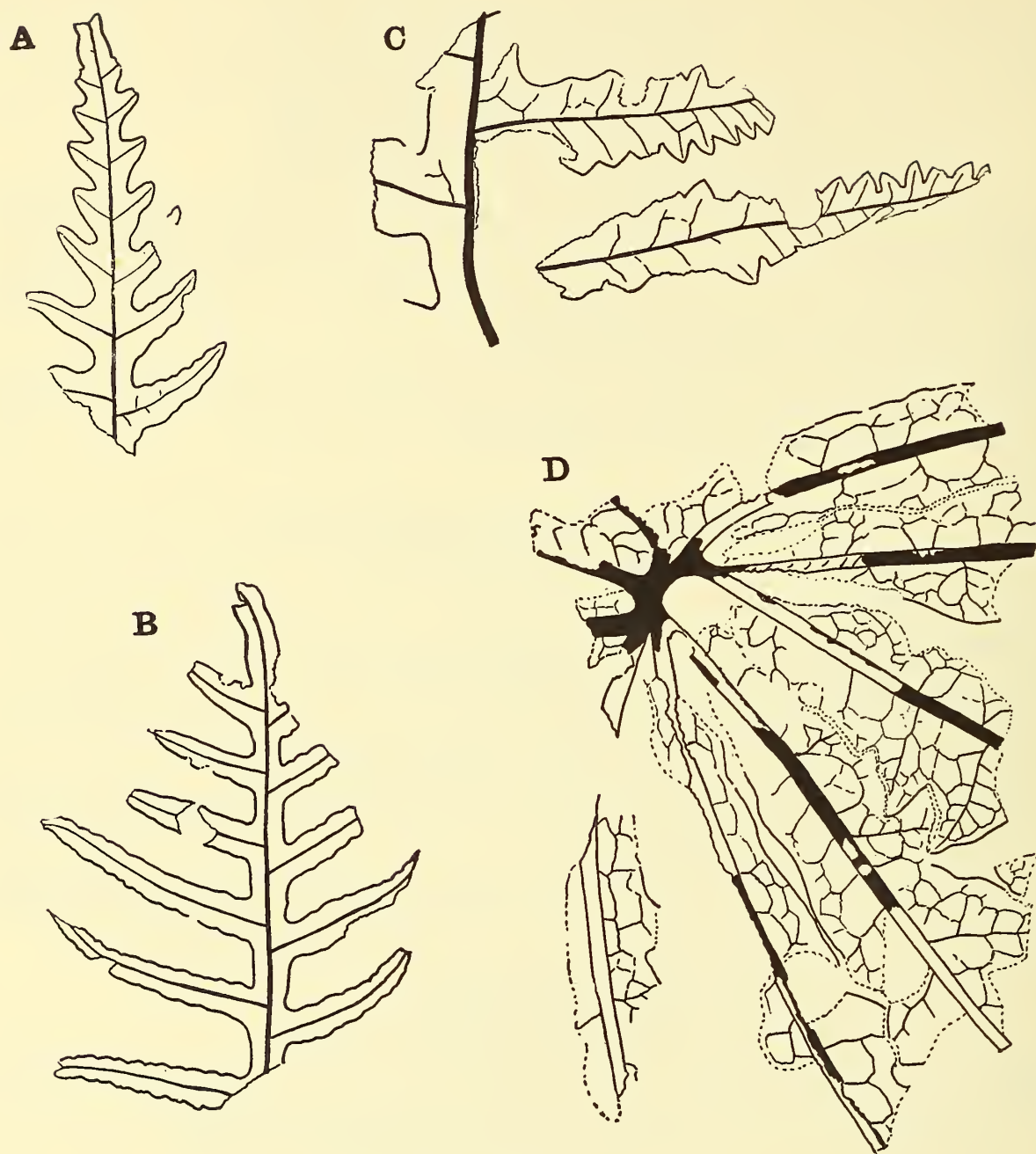


Fig. 39. *Dictyophyllum rugosum* L. & H.

A, apex of pinna, probably sterile, $\times 1$. B, apex of fertile pinna, $\times \frac{3}{4}$. C, middle part of sterile pinna (two other segments on the right are omitted), $\times \frac{3}{4}$. All three specimens in the Reed Coll., York Museum. Figures after Harris, 1944, text-fig. 1. D, leaf base, $\times 1$. Williamson Coll., 27 and 90, Manchester Museum. The rachis is not seen. Figure after Harris, 1950, text-fig. 9.

A-C, Gristhorpe Bed or Cloughton Wyke. D, ? Gristhorpe Bed.

EMENDED DIAGNOSIS. Leaf large (possibly nearly 2 m. wide). Petiole dividing into two short basal arms, each arm bearing about 4–5 pinnae at intervals of about 2 mm. Pinnae very long (estimated length nearly 1 m.). Pinna rachis stout, up to 3 mm. thick, lamina and pinnules attached laterally, surface of pinna rachis bulging on both sides, finely striated longitudinally. Basal web uniting lamina of adjacent pinnae narrow. Shape of pinna as a whole lanceolate, width gradually increasing from about 1 cm. at the base to about 20–30 cm. in the middle or upper region, contracting towards the apex. Lamina undivided below; gradually developing lateral segments (pinnules); segments widely spaced at about 2–4 cm. in the middle region of pinna but gradually becoming closer towards the apex; sterile segments up to 2.5 cm. wide; fertile up to 1.5 cm.; segments connected by a web of lamina along the rachis 1–2 cm. long and as wide as the lamina of the segment, but web becoming shorter above and segments coming into contact 5–10 cm. from the apex. Segments making an angle of 80° to the pinna rachis. Margins of larger segments lobed; lobes rounded or (in largest segments) obtusely angular; lobes always becoming better developed at some distance from the pinna rachis. Segment growing narrower towards its apex; apex obtuse or acute. In fertile leaf, segments narrower and separated by wider gaps; margins usually entire, only showing slight bulges in the largest segments.

Substance of lamina thick in both sterile and fertile leaves; margins flat in sterile; reflexed in fertile leaf.

VENATION. Midrib of segments strongly marked; laterals arising at intervals of about 5 mm. and an angle of 80° and making rather irregular polygonal meshes; smaller veins forming polygons 0.5 mm. wide enclosing free vein endings; in fertile leaf free veins being the placental bundles.

Sporangia widespread in fertile leaf, or avoiding region near midrib of segment, grouped in very small and densely crowded sori of 1–4 (often 3) sporangia. Sporangia almost sessile, about 400 μ long, 300 μ wide, annulus well developed, complete, oblique; sporangia usually falling off after shedding spores. Number of spores slightly over 100. Spores tetrahedral, walls fairly thick, smooth; when vertically compressed, sides usually concave or flat. Triradiate scars well marked, bordered by strongly thickened cuticle; mean diameter about 40 μ (34 μ).

In fertile lamina, spaces between sporangia occupied by densely packed hairs; in sterile lamina, surface without hairs.

DISTRIBUTION. *D. rugosum* occurs in the Lower and Middle Deltaic, but chiefly in the Middle Deltaic. The best specimens are from the Gristhorpe Bed and the Cloughton *Solenites* Bed; more or less fragmentary specimens have been found as follows:

Middle Deltaic, Gristhorpe Series:

Gristhorpe Bed.
Cloughton, *quinqueloba* Bed.
Cloughton *Solenites* Bed.
Farndale, Low Quarter Coalpits.
Blaikey, Sledge Shoe Coalpits.
Danby, Clither Beck Coalpits.
Bilsdale, Todhill Rosy Dikes Coalpit.
Bransdale, Ouse Gill Coalpits.

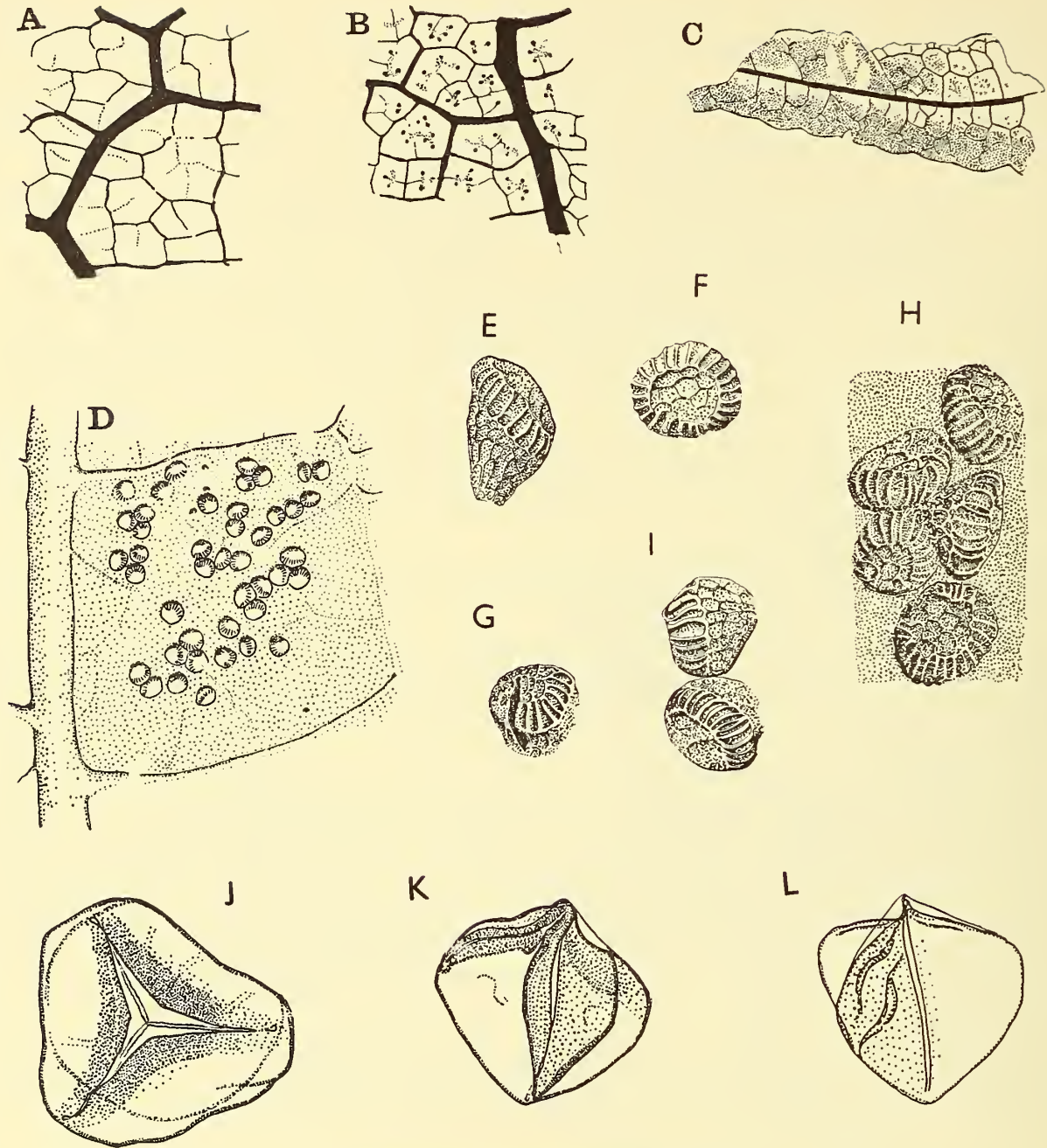


Fig. 40. *Dictyophyllum rugosum* L. & H.

A, venation of sterile part. B, venation of fertile part showing bases of fallen sporangia. Some of the small veins may have been missed. Transfer preparation V.25895b, $\times 10$. C, isolated pinna segment showing densely fertile parts (heavily stippled), moderately fertile parts (lightly stippled) and sterile parts (blank), V.25884, $\times 1$. D, one main vein-mesh from C, showing the orientation and grouping of the sporangia (impression on rock matrix), $\times 10$. After Harris, 1945, text-fig. 2. E, side view of sporangium, transfer preparation, V.26927b, $\times 50$. F, top of sporangium, transfer preparation, V.25895a, $\times 50$. G, dehiscent sporangium, transfer preparation, V.26927b, $\times 50$. H, group of three sporangia and two isolated ones, V.25892, $\times 50$. I, two neighbouring sporangia in side view, transfer preparation, V.25895a, $\times 50$. J, spore in face view, V.25884, $\times 800$. K, spore in side view, V.25884, $\times 800$. After Harris, 1945, text-fig. 3. L, spore showing the triradiate commissure, V.32101, $\times 800$. All specimens from Gristhorpe Bed.

Middle Deltaic, Sycarham Series (position uncertain):

Bransdale (or Farndale), Swinacle Coalpit.

Whitby, Long Bight fallen block, thought to be from above Eller Beck Bed.

Lower Deltaic:

Roseberry Topping.

Beast Cliff, nr. Petard Point.

Farndale, Hillhouse Nab.

DISCUSSION. Even after *Clathropteris obovata* is removed, the better specimens fall into two groups, the *rugosum* form with strongly lobed lateral segments (pinnules), and the *leckenbyi* form with entire ones. Nathorst (1880) was the first to recognise their specific identity. I am now convinced that all sterile leaves are of the *rugosum* form and all fertile ones of the *leckenbyi* form. The fertile pinnules nearly always have their sporangia facing the rock but they are to be seen where the lamina has been rubbed away, or better in transfers, when their stalks are seen even after the sporangia have fallen off.

The estimated length of a pinna of a full grown leaf is well over 50 cm. and possibly about 1 m. No fragment is more than 25 cm. long and this estimate is based as follows:

(1) The pinna rachis tapers very slightly, only about 1 mm. in 30 cm.

(2) Towards the apex the lateral segments become closer. By using (1) and (2) separate fragments can be put together to construct a whole pinna.

(3) A few slabs show fragments of two pinnae; their point of convergence marks the leaf base.

The fertile leaf was described by Thomas (1922) as 'non-soral' but it is clear that this does not mean agreement with *Platycerium* where the sori have enlarged and spread over the surface, but that the sori are very numerous and so minute and crowded as to be barely distinguishable. There is little difference apart from crowding between *D. rugosum* and *D. exile*.

COMPARISON. When *Clathropteris obovata* is excluded, *D. rugosum* becomes a well characterised species. The only specimen outside Yorkshire here regarded as probably identical is the one figured by Nathorst (1906, pl. 7, fig. 1) from Theta, Franconia. So far as is known this specimen is unique. Miss Lundblad states that there is no reason to doubt its locality. The minute fragments figured by Prinada (1938) are similar but barely determinable.

The only closely similar foreign species is *Thaumatopteris kochibei* Oishi & Yamasita (1936) from the Rhaetic of Japan (see Yokoyama, 1905 for figures). They appear to be quite different, perhaps generically, as the fertile segment of *T. kochibei* is strongly lobed and apparently has small round sori which are quite distinct; much as in *T. schenki*. The sterile leaves are very similar, but *T. kochibei* may be a smaller leaf (for the transition from widely separated to crowded pinnules at the apex occurs in about 4 cm. instead of about 15 cm.). Another difference is that the lobing on the lateral segments continues undiminished to the base, whereas in *D. rugosum* it diminishes.

The apex of the sterile pinna of *D. rugosum* looks rather like the largest (*spectabile*) form of *D. nilssoni*, but only small fragments could be confused. The spores of *D. nilssoni* have been compared in detail by Harris (1945); those of *D. nilssoni* are usually plumper with convex sides, while those of *D. rugosum* are often hollow.

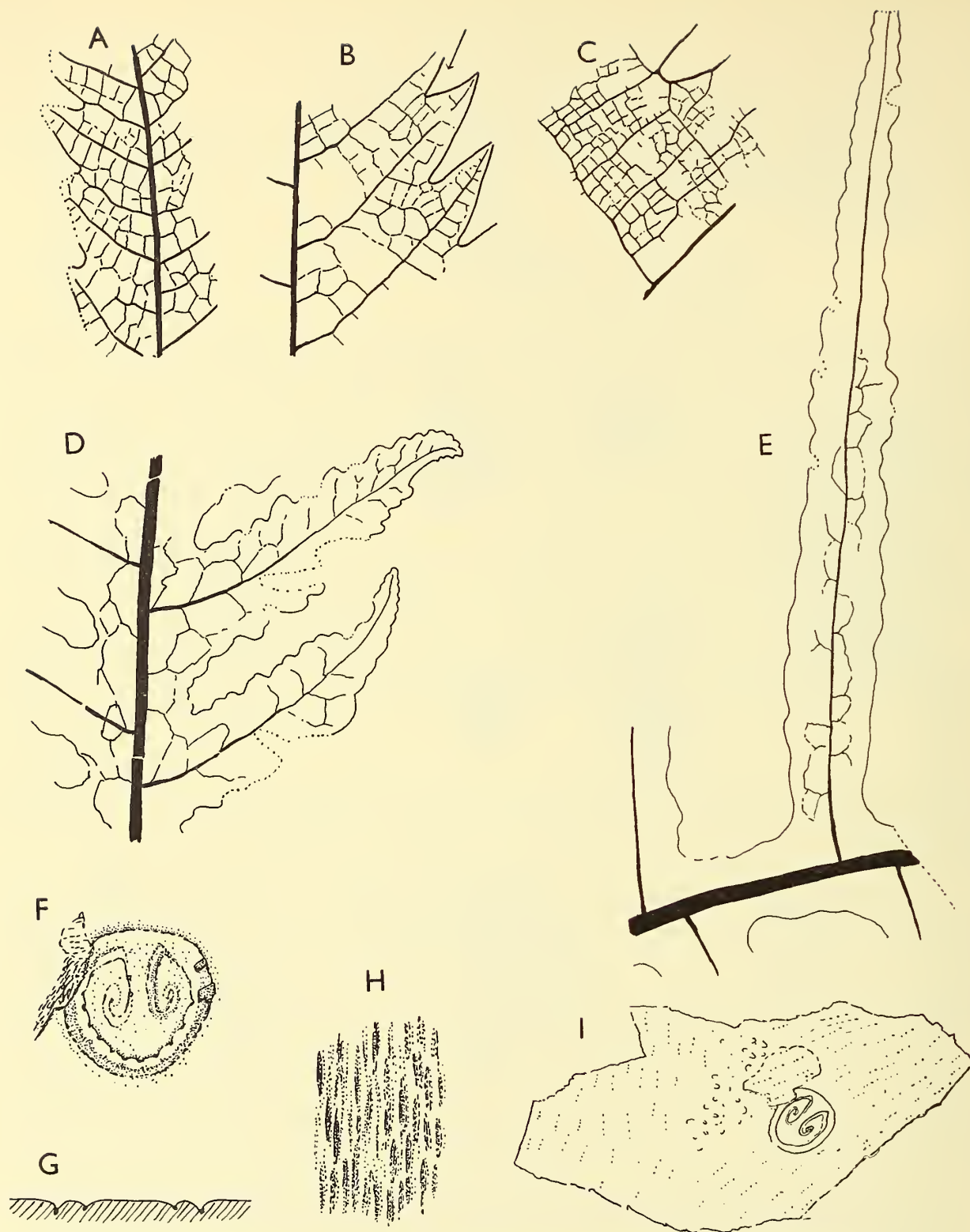


Fig. 41. *Clathropteris obovata* Oishi; *Dictyophyllum rugosum* L. & H.; Fern Rhizome.

A-C, *C. obovata*. A, specimen with rather narrow pinnae; there is a tendency to form main veins between pairs of tooth midribs. The lamina unites with the next pinna 2 cm. below this figure, V.31914, $\times 1$. B, part of a large pinna, V.31915, $\times 1$. C, details of B from the point marked with the arrow (the smallest veins occupying the meshes are obscure and have been omitted), $\times 5$. D, E, *D. rugosum*. D, from near the apex of a sterile pinna (the fragment is 16 cm. long), K.121, Sedgwick Museum, Cambridge, $\times 1$. E, fertile pinna (the specimen shows parts of seven segments), K.123, Sedgwick Museum, Cambridge. F-I, rhizome, possibly of *D. rugosum*. F, imprint of leaf scar, $\times 2$. G, imaginary section through F, taken just below the re-entrant arms to show the contour. H, cellular markings on the rhizome surface, $\times 40$. I, the whole rhizome; the direction of the striae is shown by stippling, V.32508, $\times 1$.

A, Haiburn. B, C, Hasty Bank. D, E, imperfectly localised. F-I, Cloughton *quingeloba* Bed.

A few *Dictyophyllum* leaves, e.g. *D. remauri* Zeiller (1903) have long and entire segments as in the fertile leaf of *D. rugosum*, but in none are they widely separated.

The Yorkshire *Clathropteris obovata* is distinguished in all its parts; the leafbase is less congested and the pinnae are united by a broad web of common lamina; the pinnae are rarely divided more than halfway to the midrib, the vein meshes are more rectangular and the sori form separate spots.

Fern Rhizome (? *Dictyophyllum rugosum*)

The specimen shown in Text-fig. 41 F-I is the impression of a rhizome about 4 cm. wide, showing a single very conspicuous leaf scar. The rhizome surface is finely striated (the direction of the striae is indicated by stippling) and may be at the point of branching. The only surface features are cellular ridges about 50 μ apart and of uncertain length, they are obscured in what is taken to be the angle of the branch. The substance was originally a film of coal nearly 0.5 mm. thick but has crumbled away.

The leaf base scar shows two prominent ridges (furrows in the cast), one at the outside taken to represent hypodermal fibres and the inner the xylem of the vascular tissue. This is single below (where the protoxylem masses are especially prominent) but it becomes double above (in the re-entrant arms of the C). Finer details are not clear because the surface has been slightly polished and distorted by movement during compression.

The specimen is like *Rhizomopteris schenki* Nathorst (1906) which he attributed, chiefly on the grounds of association, to *Dictyophyllum nilssoni*. It is, however, rather larger. It was found in the Cloughton *quineloba* Bed (Middle Deltaic). This bed has several species of fern leaves including *Dictyophyllum rugosum* but none that is so likely to belong to it; *Clathropteris obovata*, another leaf of nearly suitable size is unknown in this bed or indeed in the Middle Deltaic Series.

Nearly all the other associated ferns have petioles less than 12 mm. thick (several species of *Coniopteris*, *Todites princeps* and *Phlebopteris polypodioides*). *Todites williamsoni* and *T. denticulatus* have wide enough petioles and unknown rhizomes but it would be surprising if their rhizomes were of this type. Certain other ferns with wide enough petioles do occur in the Middle Deltaic but are not so far known from this bed, e.g., *Kylikopteris arguta*. The facts are inconclusive but indicate a considerable likelihood that this rhizome belongs to *D. rugosum*.

Genus CLATHROPTERIS Brongniart, 1828a:62

Clathropteris obovata Oishi

Text-fig. 42

1. Yorkshire specimens.

- 1880 '*Camptopteris whitbiensis*' Brongniart MS: Simpson in Nathorst, p. 62. (Nomen nudum.)
- 1880 '*Clathropteris whitbiensis*' Nathorst, p. 83. (Nomen nudum.)
- 1892 '*Clathropteris whitbiensis*' Fox Strangways, p. 129. (Nomen nudum.)
- 1900 *Dictyophyllum rugosum* L. & H.: Seward (in part), pp. 122, 126, pl. 18, fig. 1; text-figs. 17, 18 only. (Fig. 17 was selected as the holotype of *C. whitbiensis* (Harris, 1950).)
- 1944 '*Clathropteris whitbiensis*' Harris, pp. 662, 670. (Nomen nudum; reference to Seward's figures.)
- 1950 *Clathropteris whitbiensis* Harris, p. 1020, text-figs. 8 A-D, 9 A, B. (Diagnosis, pinna fragments, sori.)

2. Specimens from other regions.

- 1922 *Clathropteris* cf. *meniscoides* (Brongn.): Yabe, p. 11, text-fig. 8. (Leaf fragment not quite typical. Liassic; Korea.)
- 1925 *Clathropteris meniscoides* (Brongn.): Kawasaki, p. 10, pl. 13, fig. 45; pl. 14, figs. 46, 47(?), 48, 49; pl. 15, figs. 50–52. (Pinnae. Liassic; Korea.)
- 1932 *Clathropteris obovata* Oishi, p. 291, pl. 30, fig. 2; pl. 32, fig. 1. (Large part of leaf, diagnosis. Rhaetic; Japan.)
- 1936 *Clathropteris obovata* ? Oishi: Oishi & Takahasi, p. 121, pl. 1, fig. 4. (Pinna fragment. Rhaetic; Japan.)
- 1937 *Clathropteris obovata* Oishi: Brick, p. 39, pl. 12, figs. 1–6; text-fig. 18. (Good leaves including base. Central Asia.)
- 1940 *Clathropteris obovata* Oishi (exclus. synonym. partim.): Oishi, p. 214. (Discussion.)

The following cited by Oishi (1940) are excluded:

- 1907 *Clathropteris meniscoides* (Brongn.): Seward, p. 20, pl. 6, figs. 49, 50; pl. 8, figs. 75, 76. (Fragments lacking diagnostic characters. S. Russia.)
- 1938 *Clathropteris obovata* Oishi: Oishi & Huzioka, p. 78, pl. 9, figs. 1, 2. (More like *C. meniscoides* in the shallow divisions of the pinnae. Japan.)

EMENDED DIAGNOSIS. Leaf of moderate size; rachis rather slender, forking into two arms, arms bearing pinna midribs at first close together but later at intervals of 1 cm. Pinnae spreading, lamina of pinna as a whole oblanceolate, gradually increasing in width to near the apex and then contracting rather quickly. Lamina of adjacent pinnae connected for about 6 cm.; free margins strongly toothed. Divisions between teeth typically extending one third to one half the distance to the pinna rachis, rarely as much as two thirds. Teeth often curving slightly forward, apices acute, margins entire. Length of typical pinna (from basal arm of leaf) about 17 cm.; width about 6 cm. at the widest (extremes 3 cm. and 8 cm.).

Midrib of pinna slender, slightly sunken above, prominent below, not channelled; primary branch veins arising at intervals of about 1.5 cm. (1–2 cm.); arising at an angle of 50°–70° but bending forward near the base and running at 40°–50°, rarely over 60° to the midrib. Secondary branch veins tending to be almost perpendicular to the primary branches and forming a more or less rectangular mesh; finest veins tending to form square meshes enclosing blind vein-endings. Substance of lamina rather thick; margins flat or slightly reflexed; larger veins more or less sunken. Surface of lamina and midrib without hairs (apart from soral hairs). Fertile leaf similar to sterile leaf. Sori rather regularly spaced, up to 50 per sq. cm. Sori distinct, placenta prominent, bearing short, solid, strongly curved hairs. Sporangia falling after maturity (not known; spores unknown).

DISTRIBUTION. *C. obovata* is not common and is confined to the Lower Deltaic Series. The localities are as follows:

Roseberry Topping.

Hasty Bank.

Whitby (exact place unknown); probable origin of classic specimens and others in Museums.

Hawsker Cliffs: fallen block S. of Gnipe Howe.

Beast Cliff, nr. Petard Point.

Haiburn *Zamites* Bed.

Ravenscar, Peak Alum pit.

Farndale, Hillhouse Nab.

There are some good unfigured and unlocalised specimens in the Yorkshire Museum.

Outside Yorkshire this species occurs in the Rhaetic (Japan), and probably Liassic (Korea and Central Asia). The Yorkshire Inferior Oolite (Bathonian) localities are the youngest, and in fact the youngest record of the genus.

Description of Yorkshire specimens.

Seward (1900, text-fig. 17) gives an excellent impression of the specimens which Nathorst called *C. whitbiensis* except that the spots (sori) are too few. (It is not known whether this was the specimen Brongniart named *whitbiensis*.) Of Seward's other figures, pl. 18, fig. 1 is accurate but only shows the top; the pinna is 18 cm. long, the lower part being imperfect. His text-fig. 18 is accurate but does not show pieces of three other pinnae of the same leaf.

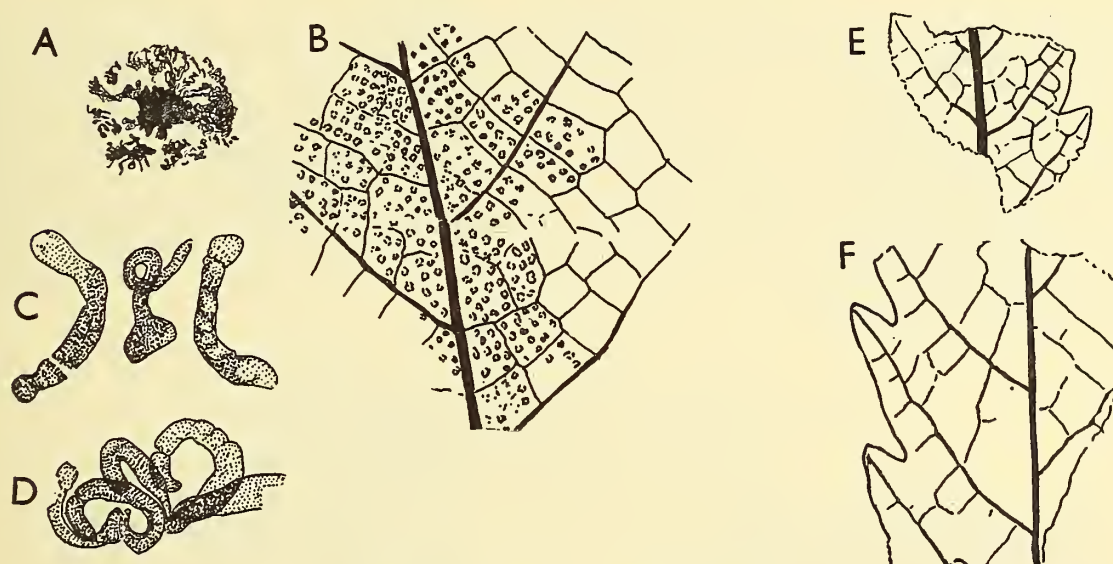


Fig. 42. *Clathropteris obovata* Oishi

A-D, figures of the Whitby Museum specimen (holotype of '*C. whitbiensis*'). A, sorus in transfer showing the placenta surrounded by small hairs, $\times 25$. B, main veins and sori, $\times 2$. C, three selected soral hairs, from transfer, $\times 200$. D, group of soral hairs, $\times 200$. E, pinna fragment, V.28312, $\times 1$. F, pinna fragment, V.28313, $\times 1$. All figures after Harris, 1950, text-figs. 8, 9.

A-D, Whitby Plant Bed. E, Hasty Bank. F, Peak Alum Pit.

A considerable number of additional specimens have been found and examined. These specimens establish the normal range of variation but do not unfortunately give the sporangia or spores. Three fertile specimens were prepared by transferring and in other ways; all the sporangia have fallen but the soral hairs are still present. Pulls and maceration of these yielded only stray spores of more than one species.

Two transfers each show a single empty sporangium, $300\mu-400\mu$ long, on the face of the fertile leaf but there is nothing to suggest attachment and they are more likely to belong to *Coniopteris*.

Identification of the Yorkshire specimens with the Asiatic.

In 1940 Oishi pointed out resemblance to certain of Seward's specimens of '*D. rugosum*' and in 1950 I stated that *C. whitbiensis* appeared close to *C. obovata*. Further material has proved them to be indistinguishable. The only apparent difference was Oishi's statement (in

his diagnosis) that the main veins make an angle of 70° to the midrib (i.e. pinna rachis). The vein angle in the Yorkshire specimens varies but is always rather more acute. Reference to Oishi's figure of the holotype (1932, pl. 32, fig. 1) shows that the angle he gives (70°) refers to the lower veins and close to the midrib; even in this specimen the veins bend forward somewhat. Other Asiatic specimens accepted by Oishi have veins at a considerably smaller angle (cf. Oishi 1932, pl. 30, fig. 2; Kawasaki 1925, pl. 13, fig. 45; Oishi & Takahasi 1936, pl. 12, fig. 4) all of which agree with what is now recognised as the normal Yorkshire form. Brick's (1937) perfect specimens of leaf bases agree with what was known from Yorkshire material.

The sporangia and spores need study before this species can be fully compared with *C. meniscoides*. The older records of *Clathropteris meniscoides* all require revision now that *C. obovata* and *C. elegans* have been described.

COMPARISON. *C. obovata* has been compared with *D. rugosum* above. The only other species of *Clathropteris* recognised, *C. meniscoides* Brongn., *C. elegans* Oishi (1940) and *C. reticulata* Kurr all differ in their shorter marginal teeth, though occasional fragments are hard to distinguish on this one character. Another difference is that the marginal teeth are usually closer in *C. meniscoides*, about 1 cm. apart; and their veins are usually straight and run at an angle of 70° – 80° to the pinna midrib. The pinnae of *C. meniscoides* are at least as wide as those of *C. obovata* and a good deal longer, so that their shape is linear-lanceolate while those of *C. obovata* approach obovate.

Genus HAUSMANNIA Dunker, 1846:12

Hausmannia dichotoma Dunker

Text-fig. 43

None of the following is from Yorkshire.

- 1846 *Hausmannia dichotoma* Dunker, p. 12, pl. 5, fig. 1; pl. 6, fig. 12. (Leaf fragments. Wealden; Germany.)
- 1871 *Hausmannia dichotoma* Dunker: Schenk, p. 223, pl. 29, figs. 8, 9. (? Fertile fragments. Wealden; Germany.)
- 1889 *Platyceriphyllum cretaceum* Velenovsky, p. 5, pl. 5, fig. 16. (Leaf fragment. Cretaceous; Bohemia. Figure reproduced in Richter, 1906, pl. 7, fig. 24, as *H. cretacea*.)
- 1892 *Hausmannia Forchhammeri* Bartholin, p. 26 (in part), pl. 11, fig. 6 only. (Leaf fragment. Liassic; Bornholm.)
- 1902 *Hausmannia Forchhammeri laciniata* Möller, p. 50, pl. 4, fig. 16; pl. 5, fig. 4 only. (Leaf fragments. Liassic; Bornholm.)
- 1906 *Hausmannia dichotoma* Dunker: Richter, p. 18, pl. 3, figs. 1–11; pl. 4, figs. 1–9; pl. 5, figs. 9–11; pl. 6, figs. 2, 5. Probably also pl. 7, figs. 12, 23, 24. (Cretaceous; Germany.)
- 1911 *Hausmannia dichotoma* Dunker: Seward, p. 657, pl. 1, figs. 14–17; pl. 2, fig. 20. (Leaf fragments. Upper Jurassic; Scotland.)
- 1948 *Hausmannia lusitanica* Teixeira, p. 34, pl. 16, figs. 5–7; pl. 17, figs. 1–8. (Good fragments. Lower Cretaceous; Portugal.)

EMENDED DIAGNOSIS (based largely on Richter's material). Rhizome slender, bearing leaves on one side. Petiole slender, rounded in section below, becoming half moon shaped in section above; dichotomising at its apex, and both halves typically dichotomising again; lamina beginning to develop at about the same level. Lamina as a whole broadly fan-shaped or funnel-shaped, up to 12 cm. from top of petiole to edge, divided by 3–5 further nearly equal dichotomies into strap-shaped segments 0.5–1.5 cm. wide, apices of segments rounded. Ultimate segments with a single midrib; midribs forking much lower than the lamina and lower and middle part of segments therefore with 2 or occasionally 4 main veins. Margins of

lamina thickened with a marginal vein. Midrib giving off lateral veins at an angle of 70° – 90° , lateral veins joining the marginal vein; laterals branching almost at right angles to form more or less square meshes, subdivided by smaller veins into ultimate meshes 0.5–1.0 mm. wide. Ultimate meshes with blind endings. Lower parts of segments sometimes showing one or two fairly strong longitudinal veins between the main veins. Fertile leaf similar to sterile, but areas between vein meshes hollowed on the under side and bulging upwards, hollowed area about 0.4 mm. wide, sharply defined. (Details of sorus not known.) Substance of lamina rather thick, veins projecting on the under side. Surfaces glabrous, apart from small hairs on the placenta of the sorus.

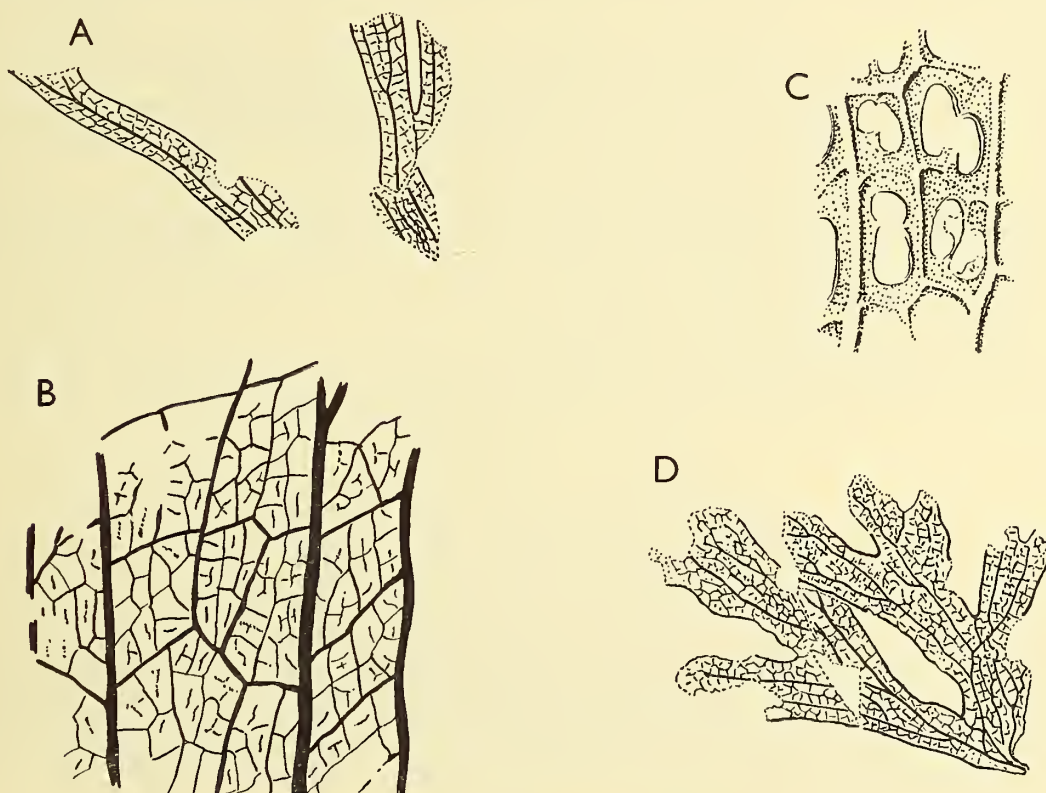


Fig. 43. *Hausmannia dichotoma* Dunker

A, three fragments, thought to be of one leaf, V.31937, $\times 1$. B, venation of sterile leaf as seen in transfer. The smallest veins are obscure and some are omitted, V.31938, $\times 5$. C, part of a fertile leaf, as seen in transfer, showing the hollow areas, V.31939, $\times 10$. D, leaf fragment, V.31940, $\times 1$.

All specimens from Roseberry Topping.

DISTRIBUTION. The Yorkshire specimens are from the Lower Deltaic Series and with the exception of one specimen from Farndale, Hillhouse Nab, all are from Roseberry Topping which belongs to the base of the Lower Deltaic (it was once suggested that the locality might be Upper Liassic).

The species is widespread in the European Lower Cretaceous and is less common earlier but is represented in the Upper Jurassic of Scotland, the Lower Oolite of Yorkshire, and at some stage in the Liassic of Bornholm.

DESCRIPTION. *H. dichotoma* is represented by a dozen very similar specimens. The preservation is imperfect as the substance has crumbled to dust. The two best specimens have been figured and several of the smaller fragments were used in the preparation of transfers in vain attempts to expose the sorus. Some of the specimens are almost certainly sterile, but others are thought to be fertile but, if so, all sporangia have disappeared before preservation. These supposedly fertile specimens have a strongly hollowed lamina in the areas enclosed by the vein meshes and this is often occupied by a pellet of rock matrix. Solution of this pellet yielded no sporangia at all.

Our ignorance of the sorus of *H. dichotoma* is outstanding for in other respects the species is very fully known. We need for this a balsam transfer of a well-preserved, nearly mature, fertile leaf.

COMPARISON. As indicated in the synonymy, *P. cretaceum* Velenovsky, *H. lusitanica* Teixeira and *H. forchhammeri* Bartholin (in part) are regarded as indistinguishable from *H. dichotoma*. There are no species which closely approach it, the nearest is *H. wilkinsi* Walkom (1928) a little known Australian species which appears to be less deeply divided. There are two leaves sometimes placed near *H. dichotoma*, but which appear to be quite different. In neither has a vein network been demonstrated. These are: *H. minuta* Richter, a *Baiera*? and *Asplenium brongniarti* Debey & Ettingshausen, a *Sphenopteris*?

The other section (*Protorhipis*) of *Hausmannia* consists of leaves with a more or less entire lamina, never completely divided. Many species have been named (more than can be distinguished) but none could provide fragments matching the Yorkshire ones.

Family SCHIZAEACEAE

Genus KLUKIA Raciborski, 1890:5

EMENDED DIAGNOSIS. Leaf Pecopterid, finely divided, sterile and fertile leaves similar. Sporangia on under side of fertile pinnule, borne singly on lateral veins, oval, attached laterally, annulus circular, uniseriate, at the inner end. Sporangium dehiscing longitudinally, remaining attached after shedding spores. Spores triradiate, strongly sculptured.

Klukia exilis (Phillips) Raciborski

Text-figs. 44-46

1. Yorkshire specimens.

- 1829 *Pecopteris exilis* Phillips, p. 148, pl. 8, fig. 16. (Poor figure of fertile fragment.)
- 1833 *Pecopteris phillipsi* Brongniart, p. 304, pl. 109, fig. 1. (Large sterile leaf, not typical.)
- 1835 *Sphenopteris serrata* Lindley & Hutton, p. 187, pl. 148. (Sterile leaf, attributed by Harris (1947) to *Coniopteris arguta*.)
- 1837 *Pecopteris obtusifolia* Lindley & Hutton, p. 15, pl. 158, figs. 1, 1a, 1b (non pl. 157, fig. 1c). Fertile leaf.
- 1851 *Pecopteris exilis* Phillips: Bunbury, p. 188, pl. 13, fig. 5. (Fertile fragment, sporangia.)
- 1890 *Klukia exilis* (Phillips) Raciborski, p. 6. (Name only; pl. 1, figs. 16-19 represents another species.)
- 1894 *Klukia exilis* (Phillips): Seward, p. 197, text-figs. 1-5. (Fertile fragments, sporangia.)
- 1900 *Klukia exilis* (Phillips): Seward, p. 130, pl. 16, fig. 7. (Fertile fragment.)
- 1946 *Klukia exilis* (Phillips): Harris, p. 357, text-figs. 1-3. (Sterile and fertile, sporangia, spores.)

2. Specimens from other regions.

- 1907 *Klukia exilis* (Phillips): Seward, p. 4, pl. 1, figs. 4-7; pl. 3, fig. A. (Fertile fragment. Turkestan.)
 1912 *Klukia exilis* (Phillips): Seward, p. 11, pl. 2, figs. 20, 21; pl. 6, fig. 81; pl. 7, fig. 88. (Fertile fragments, sporangia. Afghanistan.)
 1933 *Klukia marginata* Prinada, p. 6, pl. 1, figs. 1-6. (Good sterile and fertile fragments. Jurassic; Transcaucasia.)
 1938 *Klukia exilis* (Phillips): Prinada, p. 368, text-fig. 1. (Ill-preserved fertile pinnule. Jurassic; Russia.)
 1952 *Klukia exilis* (Phillips): Endo, p. 165, pl. 1, figs. 1-4; text-fig. 1. (Fertile, sporangium. Japan.)
 1957 *Klukia exilis* (Phillips): Stanislavski, p. 33, pl. 5, figs. 1-3; text-fig. 7. (Fertile fragments. S. Russia.)

3. The following represent a distinct species:

- 1894 *Klukia exilis* (Phillips): Raciborski, p. 23, pl. 7, figs. 13, 14, 17; pl. 8, figs. 1-3, 7, 8, 9b; pl. 9, figs. 1, 2; pl. 26, fig. 1.
 1894 *Klukia exilis* var. *parvifolia* Raciborski, p. 25, pl. 8, fig. 6; pl. 26, fig. 2.
 1894 *Klukia acutifolia* (L. & H.): Raciborski, p. 26, pl. 7, figs. 10-12, 18.
 1894 *Klukia Phillipsi* (Brongn.): Raciborski, p. 27, pl. 8, figs. 4, 5; pl. 7, fig. 16.
 (All fine material from the Middle Jurassic of Poland.)

4. Sterile specimens barely determinable or definitely distinct from *Klukia exilis*:

- 1913 *Cladophlebis* (*Klukia*) *exilis* (Phill.): Halle, p. 17, pl. 1, fig. 25. (Middle Jurassic; Graham Land.)
 1916 *Klukia exilis* (Phillips): Kryshstofovich, p. 97, pl. 7, figs. 4-6, 8. (Ussuriland.)
 1919 Cf. *Pecopteris exilis* (Phillips): Antevs, p. 18, pl. 1, fig. 16 (different); fig. 17 (indeterminable). (Lower Lias; Sweden.)
 1922 Cf. *Pecopteris exilis* (Phillips): Johansson, p. 13, pl. 5, figs. 10, 11. (Rhaetic; Sweden.)

5. The following records have been given without figures:

- 1900 *Pecopteris exilis* Phillips: Zeiller, p. 2. (Madagascar.)
 1908 *Klukia exilis* (Phillips): Krasser, p. 441. (Lower Lias; Austrian Alps.)
 1911 *Klukia exilis* (Phillips): Thomas, pp. 12, 60. (Jurassic; Kamenka, Russia.)

EMENDED DIAGNOSIS. Lamina as a whole probably lanceolate, width 20 cm. or more, apex acute (base and petiole unknown, length unknown). Leaf, bipinnate with deeply pinatifid segments (nearly tripinnate). Rachis slender, up to 3 mm. wide; pinnae of first order typically widely spaced, often subopposite; arising at an angle of about 50°, shape as a whole symmetrical, linear-lanceolate (length 4-5 times the width). Secondary branches typically 3 cm. long, arising at an angle of 60°-70°. Tertiary lobes (pinnules) oblong to deltoid, typically 2.5-4.0 mm. long, nearly 1.0 mm. wide near the base, apex obtuse or rounded; margins entire, adjacent pinnules connected by a web of lamina 0.5 mm. wide. Primary and secondary rachises smooth, with a sharply defined channel above. Branching katadromic throughout (i.e. the first pinna or pinnule arising on the basiscopic side). Pinnules on the two sides of a pinna equal or lower basiscopic ones short.

Surface of sterile pinnules convex but midrib depressed, margins curved downwards but not curved back under the lamina. Lateral veins typically simple, arising at intervals of about 0.5 mm. and an angle of about 60°; veins once forked in the largest pinnules. Under surface finely tomentose.

Fertile pinnules usually completely fertile from base to apex, typically bearing 6-14 sporangia, appearing narrower than sterile because margins are everywhere sharply incurved. Lateral veins simple, each bearing an elliptical sporangium 0.5 mm. long; annulus cells about 16. Under surface covered with a dense but fine tomentum usually concealing the veins and often parts of the sporangia. Spores 150-400 per sporangium, typically 60μ wide (extremes

35 μ and 80 μ). Dorsal surface rounded, ventral with long triradiate cracks and flat facets. Margins of triradiate cracks often raised, no arcuate ridges present. Dorsal surface very thickly cutinised, marked with deep pits, walls separating three pits often raised to form a rounded lump; walls separating two pits often broken by a low channel connecting the pits. Facets less thickly cutinised, surface bearing many small warts, separate or united in groups.

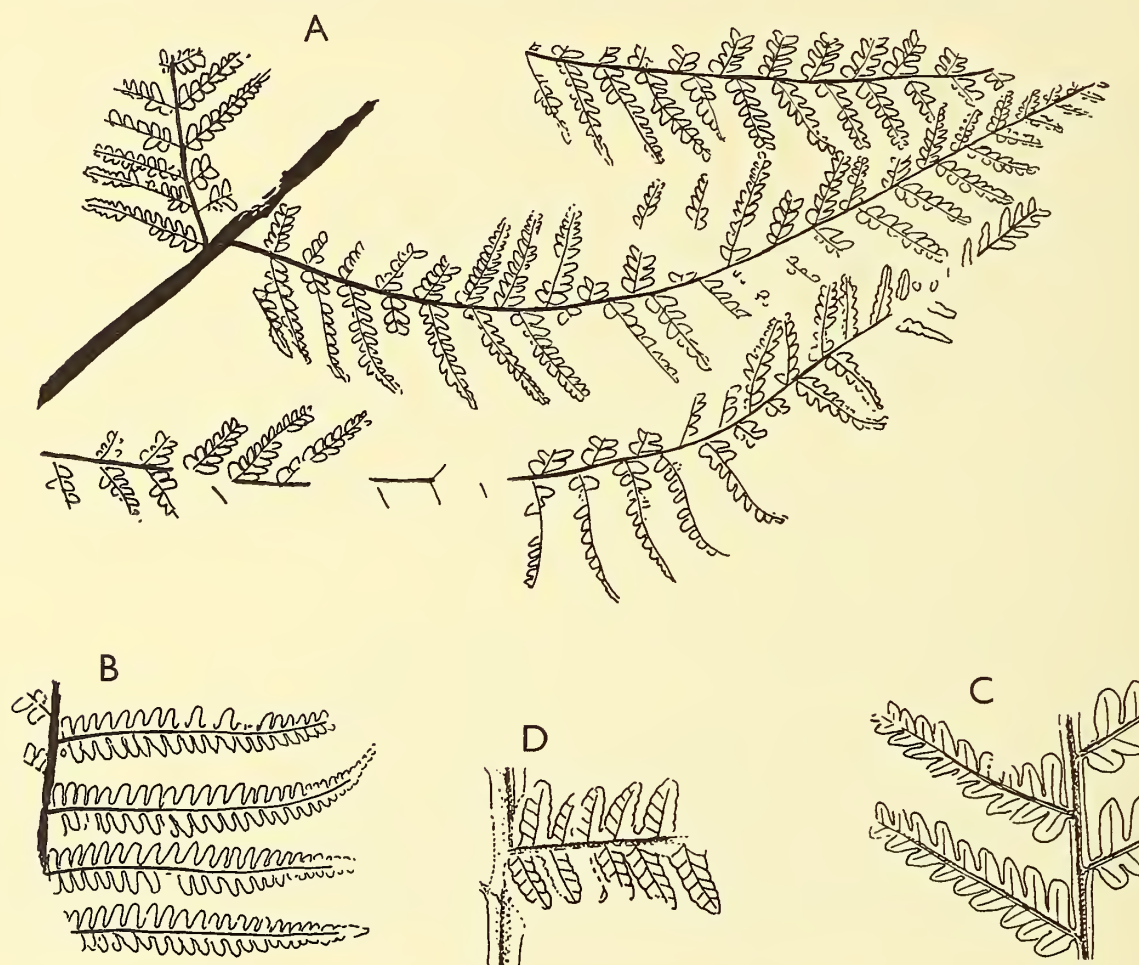


Fig. 44. *Klukia exilis* (Phillips), sterile leaves

A, small leaf (lowest pinnae omitted). Leckenby Coll., K.101, Sedgwick Museum, Cambridge, $\times 1$. B, single pinna from large leaf (part omitted). Leckenby Coll., K.85, $\times 1$. C, details from a lower pinna of K.101 (not included in A), $\times 2$. D, details from the leaf shown in B, $\times 2$.

All the above are probably from the Gristhorpe Bed.

DISTRIBUTION. All the earlier figured Yorkshire specimens and all the old Museum specimens seem to be from the Middle Deltaic Gristhorpe Bed, where the species is common at a few points. It is also locally common in the Cloughton *Solenites* Bed (especially in blocks fallen from the cliff). It is common also at two Lower Deltaic localities, Beast Cliff *Otozamites* Bed, and Beast Cliff *Ptilophyllum* Bed. Isolated spores like those of *K. exilis* (but barely distinguishable from those of *Stachypteris*) occur fairly widely in macerations.

There is good material of *K. exilis* from Yorkshire in the Museums of York, Oxford and Cambridge.

Outside Yorkshire *K. exilis* occurs in Middle Jurassic rocks of Russia, Central Asia and Japan.

DISCUSSION. Although there are many fine specimens of *Klukia exilis* from Yorkshire in old Museum collections, they have not been figured. Only small fragments have been

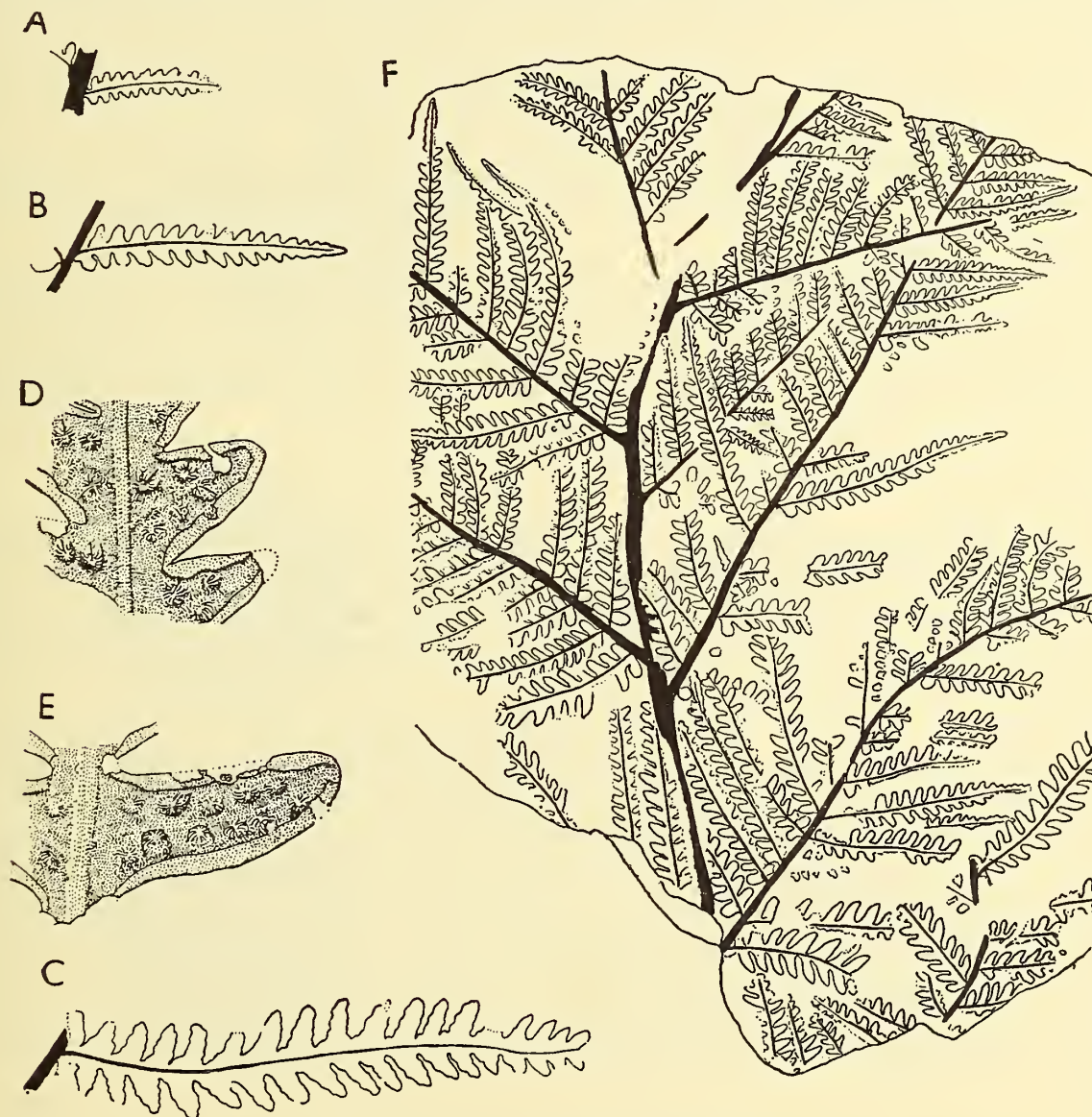


Fig. 45. *Klukia exilis* (Phillips), fertile leaves

A-C, details of different parts of the specimen shown in F, $\times 2$. D, E, balsam transfers of fertile pinnules showing the reflexed margins and sporangia almost buried in hairs, V.26902-03, $\times 8$. F, fragment from normal sized leaf (about 1 cm. at each side omitted). The lower pinnae are fertile, the upper sterile. Leckenby Coll., 91, Sedgwick Museum, Cambridge, $\times 1$.

All figures after Harris (1947) and represent specimens believed to be from Gristhorpe Bed, but the localisation of F is imperfect.

represented and Raciborski's beautiful figures have been taken as typical *K. exilis*. I am, however, convinced that most, and probably all of his specimens are distinct.

The Yorkshire specimens are numerous enough to indicate what is the normal form of the leaf: most specimens are in fact close to Text-fig. 45 F; a few fragments of larger leaves have been seen, Text-fig. 44 B, and also of smaller leaves, Text-fig. 44 A.

More than half the fragments are fertile and in a surprising proportion cleavage exposes the sporangia; the best details are, however, only seen in balsam transfers, where the reflexed margins and tomentum are always seen. Where the cleavage exposes the upper surface this either shows slight bulges or dimples over the sporangia, the difference being readily explicable on Walton's theory of collapse in compression.

A previous account (Harris, 1946) is here corrected in one particular; it is only the fertile pinnules which have reflexed margins, the margins of the sterile pinnules being merely bent downwards.

The spores have been prepared from almost every fertile specimen and prove very uniform and well characterised. The only exception is the unusual specimen shown in Text-fig. 46 E, F which yielded a proportion of small and distorted spores among normal ones. A few specimens are unripe, here the spores are of fairly normal size but the walls are a little less thickly cutinised and it is impossible to isolate them by maceration.

Ignorance of the lower part of the leaf of *K. exilis* is an obvious gap in our knowledge of the Yorkshire material.

An interesting fragment found by Dr. H. H. Thomas at Gristhorpe has been pyritised and appears to have been preserved without compression. In this specimen the substance of the lamina is thick and the margins project downwards and only slightly inwards, not being sharply infolded as the compressions suggest. The sporangia point downwards and inwards, the annulus being well exposed.

COMPARISON. There are fine Polish specimens of *Klukia* which probably represent another species, but it has as yet no specific name (Raciborski 1894, material described and figured under *K. exilis*, *K. exilis parvifolia*, *K. acutifolia*, *K. phillipsi*). While some of the less characterised specimens are fairly like Yorkshire ones, others are outside their range of variation. These include pl. 8, fig. 1 (rachis far thicker, not channelled; pinnae alternate, secondary pinnae arising at right angles; pl. 7, fig. 16 (primary and secondary pinnae at right angles). Many specimens show longer pinnules (pl. 7, fig. 17; pl. 26, fig. 1) and the number of sporangia may be greater (pl. 8, fig. 4). In none of the fertile pinnules is the margin shown as reflexed. It is assumed that the whole material represents one new species, but a new name should not be given without a reinvestigation of the material and, if possible, examination of spores.

Klukia marginata Prinada is *not* distinct from *K. exilis*; in the absence of adequate figures of the Yorkshire type material, Prinada used Raciborski's figures and so the reflexed margin in his pinnules was taken as a distinguishing character.

Two very incompletely known Japanese species are *K. yokoyamae* (see Oishi 1939, 1940) which has rather longer pinnules than *K. exilis*, and *Cladophlebis* (*Klukia*) *koraiensis* Yabe which, as Oishi (1940) remarks, looks like *K. exilis*. *K. yokoyamae* may perhaps belong to the same species as Raciborski's material.

It was suggested (Harris, 1946: 363) that there was a second Yorkshire species of *Klukia*. On further investigation it is apparent that the specimens are merely extreme forms of *K. exilis*. Records of purely sterile material have been rejected as the sterile leaf of *K. exilis* is by no means well characterised.

Sterile fragments from Yorkshire have been much confused with *Kylikipteris* (*Coniopteris*) *arguta* and the specific names *arguta*, *exilis*, *acutifolia*, *obtusifolia*, *serrata* and *lindleyi* have been applied to Museum specimens indiscriminately. They are often very difficult to separate but

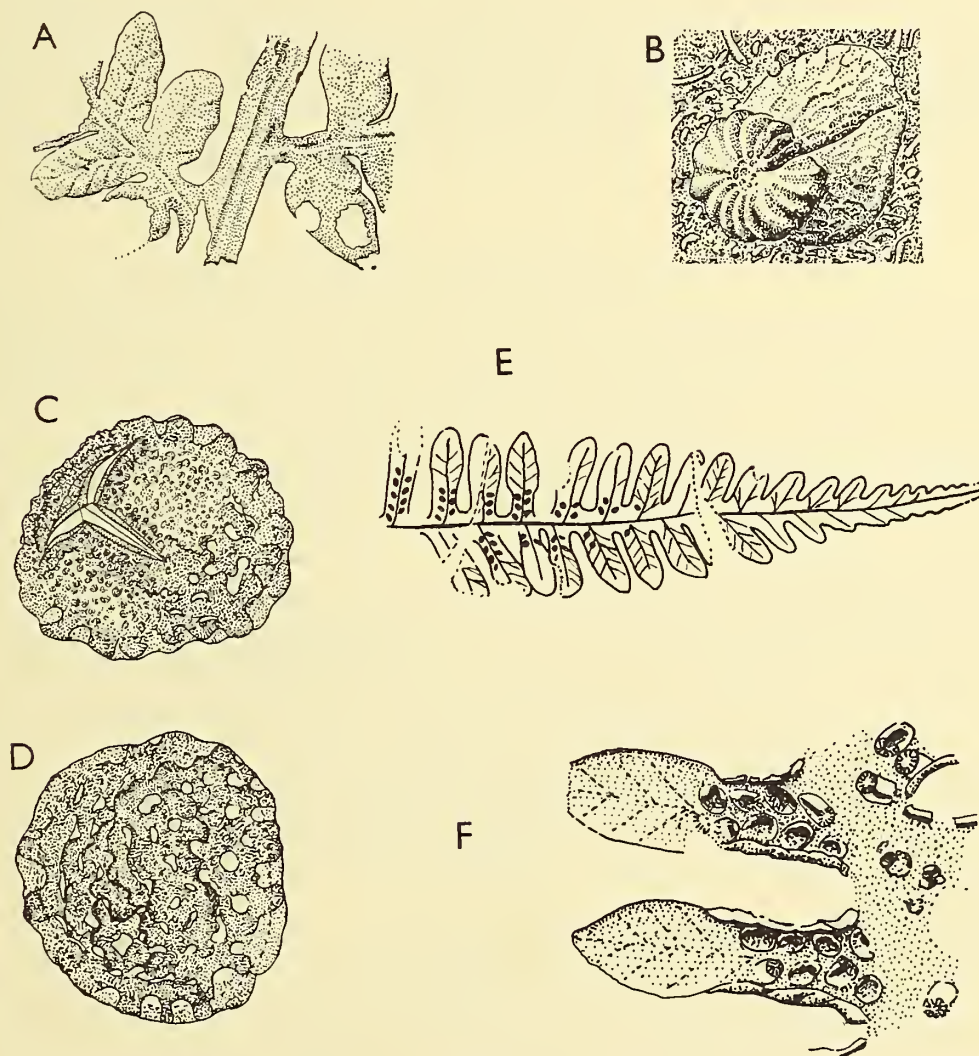


Fig. 46. *Klukia exilis* (Phillips)

A, surface of sterile pinnules showing channelled pinna rachis and slightly grooved pinnules. Leckenby Coll., 86, Sedgwick Museum, Cambridge, $\times 4$. B, sporangium, from a transfer, V.26903, $\times 50$. C, ventral side of a spore. D, dorsal side of another spore, V.25840, $\times 500$. E, isolated secondary pinna of unusually large size, partly fertile, V.31973, $\times 1$. F, transfer of a similar pinna showing the contraction of the fertile parts by curving of the leaf margin. (The veins are seen by transmitted light.) V.31973a, $\times 4$. A-D are taken from Harris, 1946, text-fig. 3. E, F, are from Beast Cliff *Otozamites* Bed.

I believe the whole leaves are quite different; that of *K. arguta* being larger and once more pinnate. Differences recognisable in fragments are:

In *Klukia exilis* all rachises are sharply channelled above, in *K. arguta* they are usually convex above and where they are hollow it is probably because of collapse of the tissues. In *K. exilis* also the pinnule margins are more depressed and the under side is tomentose (both characters seen in balsam transfers). In *Kylikopteris arguta* the margins are only slightly bent and the under side is smooth. The veins are usually simple in *K. exilis* but forked in *Kylikopteris arguta*.

Sterile fragments of *K. exilis* are also similar to *Aspidistes thomasi* but again there is a difference in the margins and covering of the under surface. *K. exilis* rarely shows the rounded pinnule lobes seen normally in *A. thomasi*. Several species of finely divided fern leaves, which approach sterile *K. exilis* rather closely, have been described under various names. In the absence of information about fine details it is useless to discuss their possible identity.

Genus STACHYPTERIS Pomel, 1849:336

EMENDED DIAGNOSIS. Sterile and fertile leaves similar, repeatedly pinnate. Fertile parts spike-like, terminal on a rachis branch; dorsiventral, consisting of a series of reduced pinnules above and with two rows of sporangia below. Sporangium with a well-developed annulus running obliquely in its exposed part. Spores strongly sculptured.

DISCUSSION. *Stachypteris* is one of the most interesting Mesozoic ferns as there is still doubt about its morphology. Its sterile leaf is unremarkable, but its little cone-like fertile appendages look unique.

Pomel (1849) thought the terminal spikes were like the fertile pinnules of *Lygodium* (and this is my view also). Saporta (1872, 1891) with fresh material, believed it was a Polypodiaceous fern near *Cheilanthes* or *Onychium*, but no one has since held that view. Thomas (1912), the first to examine the sporangia microscopically, left its classification open but pointed out resemblances both to *Lygodium* and to the Cyatheaceae. Bower (1926) basing his views on one only of Thomas' figures, dismissed the *Lygodium* view and supported a close relationship to the Loxsomaceae, a family with marginal gradate sori. Hirmer (1927) accepted Bower's view. Turutanova-Ketova (1929, 1930), who described new material, strongly supported the Loxsomaceous affinity.

I have been aided in this investigation by being able to study the whole of the Yorkshire material, through the kindness of Dr. H. H. Thomas and of the Director of the Swedish Museum of Palaeobotany. Unfortunately the species is rare in Yorkshire and it has not been possible to treat the scanty material as drastically as I would have wished. I have been forced to leave the sporangia undescribed. It is certain, however, that their arrangement is as in *Lygodium* and has nothing to do with a Loxsomaceous sorus. *Stachypteris* either belongs to the Schizaeaceae or to a new family.

The affinities of *Stachypteris* are discussed at the end of the description of the specimens.

Seven Jurassic species have been distinguished by name but they may all be united under *Stachypteris spicans* for their distinguishing characters are only of the kind which distinguish the different parts of a single finely divided fertile fern leaf.

Stachypteris spicans Pomel

Text-figs. 47, 48

1. Yorkshire specimens.

- 1912 *Stachypteris hallei* Thomas, p. 610, pl. 4. (Sterile and fertile fragments, sporangia, spores. Yorkshire.)
 1926 *Stachypteris hallei* Thomas: Bower, p. 258. (Genus discussed in relation to *Loxsonia*.)

2. Specimens from other regions.

- 1849 *Stachypteris spicans* Pomel, p. 336. (No figure. France.)
 1849 *Stachypteris litophylla* Pomel, p. 337.
 1849 *Stachypteris pulchra* Pomel, p. 337.
 1872 *Stachypteris spicans* Pomel: Saporta, p. 383, pl. 49, figs. 2-6. (Sterile and fertile. Corallian; France.)
 1872 *Stachypteris litophylla* Pomel: Saporta, p. 387, pl. 50, figs. 1-5. (Sterile and fertile. Corallian; France.)
 1872 *Stachypteris minuta* Saporta, p. 390, pl. 51, fig. 1. (Sterile fragments. Kimeridgian; France.)
 1891 *Stachypteris spicans* Pomel: Saporta, p. 435, pl. 289, fig. 1; pl. 290, fig. 4. (Sterile and fertile, some details of spike. Kimeridgian and Corallian; France.)
 1891 *Stachypteris litophylla* Pomel: Saporta, p. 438, pl. 289, fig. 2; pl. 290, figs. 1-3. (Sterile and fertile. Corallian; France.)
 1891 *Stachypteris minuta* Sap.: Saporta, p. 440, ? pl. 277, figs. 5, 6; ? pl. 290, figs. 5, 6; pl. 291, figs. 8-10. (Sterile and fertile. Kimeridgian, Corallian and Sequanian; France.)
 1929 *Stachypteris turkestanica* Turutanova-Ketova, p. 142, pl. 1, figs. 1, 2; text-figs. 1, 2. (Good fertile leaf. Jurassic; Turkestan.)
 1929 *Stachypteris turkestanica elongata* Turutanova-Ketova, p. 143, pl. 2, figs. 5, 6. (Fertile fragment. Jurassic; Turkestan.)
 1930 *Stachypteris elongata* Turutanova-Ketova, p. 137, pl. 1, fig. 2. (Fertile fragment. Middle Jurassic; Turkestan.)
 1930 *Stachypteris* sp., Turutanova-Ketova, p. 136, pl. 1, fig. 3. (Small fragment. Jurassic; Turkestan.)

The following are all sterile and are considered distinct:

- 1894 *Stachypteris minuta* Sap.: Saporta, p. 48, pl. 4, figs. 1, 10. (Sterile. Portugal; referred to '*Davallia delgadoi*' by Teixeira, 1948, p. 27.)
 1894 *Stachypteris litophylla* Pomel: Saporta, p. 48, pl. 6, fig. 14. (Sterile. Portugal; doubtfully referred to *Scleropteris sinuata* by Teixeira, 1948, p. 29.)
 1909 *Stachypteris litophylla* Pomel: Salfeld, p. 10, pl. 3, fig. 4; pl. 4, fig. 16. (Sterile leaves. Corallian; N. Germany; perhaps the same as '*Cladophlebis* cf. *Moisseneti*' of same locality.)

It should be noted that certain sterile leaves described by Saporta (1872, 1891) under other names such as *Scleropteris tenuisecta*, *Sphenopteris minutula* and *Hymenophyllites delicatulus* are similar to those of *Stachypteris spicans*.

EMENDED DIAGNOSIS. Sterile and fertile leaves similar in shape. Lamina (or known part of lamina) at least 12 cm. × 10 cm., broadly triangular; petiole unknown. Leaf 3-4 times pinnate, main and branch rachises solid (not channelled) slender, smooth; branch rachises arising at a wide angle. Ultimate branches (primary, secondary or tertiary) if fertile ending in a 'fertile spike'. Branching katadromic throughout (first pinna or pinnule on basiscopic side). Pinnules (ultimate branches of sterile part) typically oval or lanceolate, 1 mm. long, 0.75 mm. broad, but sometimes larger and partly divided and with branched veins, smaller pinnules with a single vein at about 45° to the pinna midrib. Substance of lamina thick, merging imperceptibly into rachis branches, veins not prominent but shown by elongated epidermal cells or as a very slight groove. Lamina not cutinised, its margins not specialised, surfaces of lamina and rachis branches without scales or hairs.

Fertile spike terminal on a rachis branch, usually separated by a slight stalk from the sterile parts below. Fertile pinnules arising alternately, smaller than sterile, but basal ones sometimes

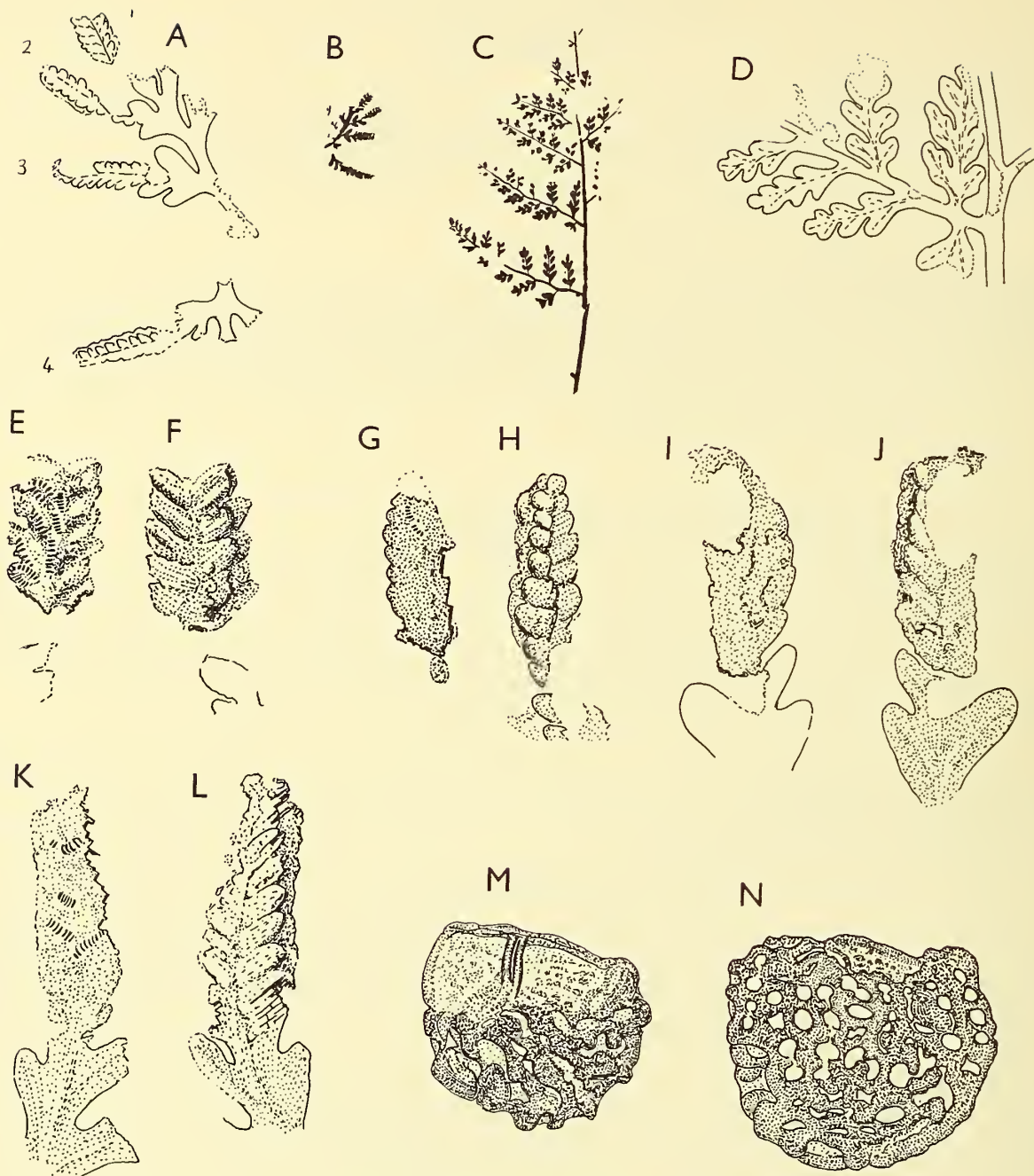


Fig. 47. *Stachypteris spicans* Pomel

A, transfer of fertile fragment, V.31908, $\times 4$. The spikes (1-4) are shown in detail below. B, the same fertile fragment as originally seen, $\times 1$. C, sterile fragment, V.31909, $\times 1$. D, details of part of C, $\times 4$. E, F, direct view and transfer of spike (1), V.31908, $\times 10$. G, H, direct view and transfer of spike (2), V.31908, $\times 10$. I, J, direct view and transfer of spike (3), V.31908, $\times 10$. K, L, direct view and transfer of spike (4), V.31908, $\times 10$. M, N, two spores, from the preparation made by Thomas (1912, pl. 4, fig. 5), V.27708a, $\times 500$.

All the above are from Marske Quarry.

transitional, typically 0.7 mm. long and 0.3 mm. wide, ovate or triangular, attached by a broad base, margins partly united with those of neighbouring pinnules, surface convex, substance thick, midrib simple. Sporangia forming two rows, situated on lower side of fertile spike, probably one below each fertile pinnule. Form of sporangia unknown but annulus conspicuous, lying obliquely in relation to the spike axis. Spore output possibly about 100.

Spores 40μ – 80μ wide (typically about 50μ). Dorsal side very thick walled, rounded, ventral thinner, flattened, with three flat facets. Dorsal side marked with deep pits separated by ridges which anastomose irregularly, neighbouring pits often connected by a narrow channel. Facets bearing small tubercles. Triradiate ridges about 80 per cent of the spore radius, rather prominent.

DISTRIBUTION. *Stachypteris* is rare in Yorkshire and is recorded from the Lower Deltaic Series only. Apart from a few sterile fragments of rather doubtful determination there are one sterile and three fertile leaves from Marske Quarry and one from Whitby.

S. spicans appears to be common in the Upper Jurassic, the Corallian and Kimeridgian of Western France. The Yorkshire specimens come from the bottom of the Lower Deltaic and are thus rather older. The age of the specimens from Turkestan is merely given as Jurassic.

As mentioned in the synonymy the determinations of sterile specimens from Germany and from Portugal are rejected.

DESCRIPTION AND DISCUSSION. The best sterile leaf (V.31909) is shown in Text-fig. 47 C, D. The substance is rather thick and opaque and the veins are only faintly indicated by the surface cells. The specimen was untreated apart from cleaning.

V.27708 is a small fertile fragment which has deteriorated, probably through oxidation before it was collected. It shows sporangia much as in V.31908. A crumb when macerated gave no spores.

V.31908, another fertile fragment, is figured here in detail. The under side was exposed. This was drawn as fully as the rather poor preservation allowed; three of the four spikes showed traces of annulus cells though none is distinct. It was then transferred to expose the upper side. No sporangia are now seen, but instead the very conspicuous fertile pinnules (tilted in Text-fig. 47 H).

It will be seen that while in the direct view the four spikes give some, or even considerable indication of the annulus cells of sporangia; in the transfer no trace of annulus is seen but instead little lobes of thick coaly matter which probably represent reduced fertile segments. These lobes show faint longitudinal cells but no other features. A few minute fertile fragments were macerated but only stray spores of various sorts were found and it is presumed that the sporangia had dehisced.

Many *Stachypteris* spores and some others were isolated from the matrix when this specimen was transferred.

V.27708. This Marske specimen which Thomas (1912) chose as the holotype of *S. hallei* is better preserved. It has been redrawn (Text-fig. 48 C) because a few more details became visible when it was further cleaned, but the drawings given by Thomas are excellent. All of the numerous fertile spikes are like the one drawn by him and show the ultimate rachis continuing as a groove up the spike without interruption. There is a slight interval between the upper sterile pinnules and the lowest lobe (fertile pinnule) of the spike, but the alternating sequence is maintained. Not one of the spikes shows any annulus on its surface, but there are

suggestions of a vein down the middle of the fertile pinnules. In places the coaly matter of a spike has flaked away and the imprint of annulus cells is clear. A few minute fragments were macerated but these were without spores; a number of *Stachypteris* spores were noted in the matrix under one of the spikes and Thomas made his spore preparation from this specimen. Most of the sporangia are presumed to have dehisced.

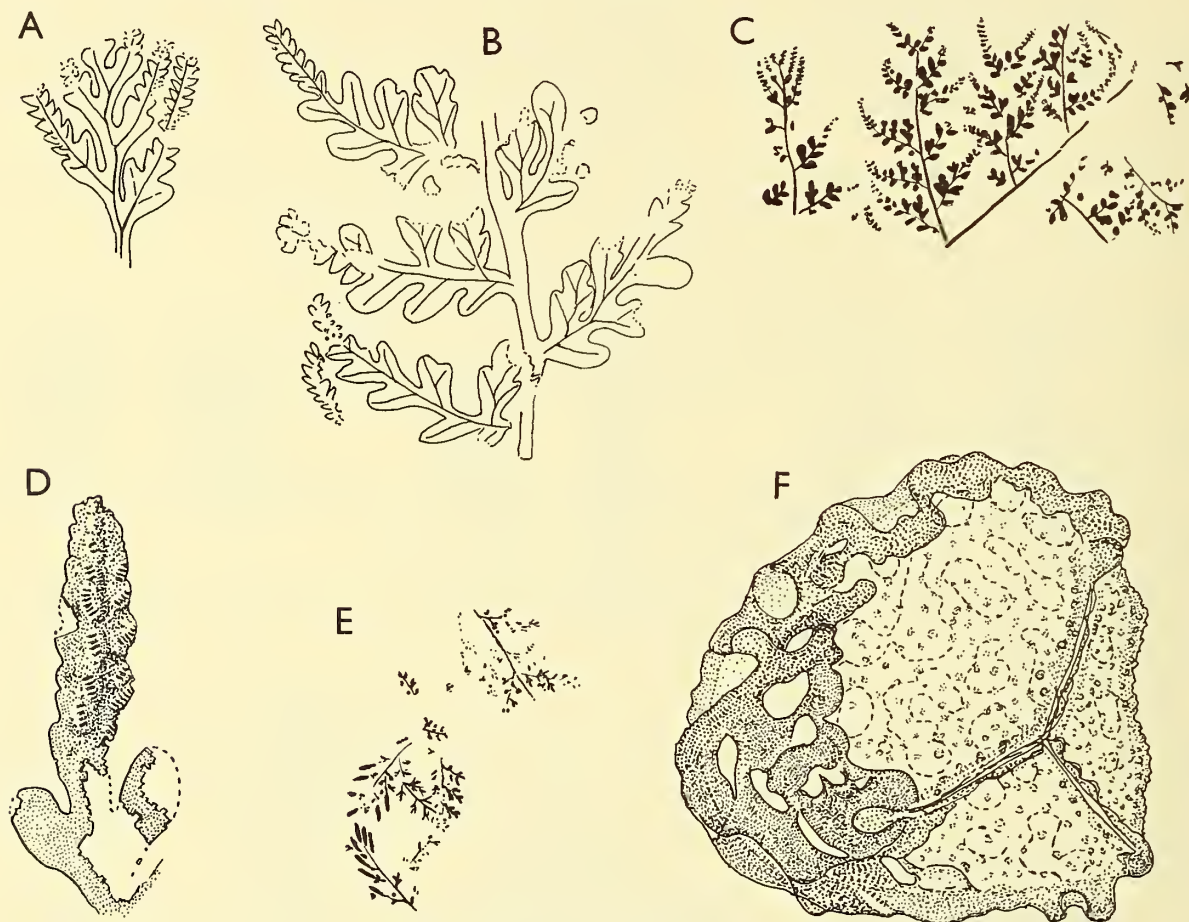


Fig. 48. *Stachypteris spicans* Pomel

A, B, details from C, $\times 4$. C, fertile leaf, V.27708, $\times 1$. Also figured Thomas, 1912, pl. 4, fig. 1. D, fertile spike (bottom left in E), $\times 10$; dotted lines represent restored outline not visible in specimen; figured Thomas, 1912, pl. 4, fig. 4. E, various leaf fragments of Halle's Whitby specimen (two on left are fertile, rest sterile); different fragments are shown in Thomas (1912, pl. 4, figs. 2, 2a, 3, 3a). F, isolated spore of rather large size; the pits on the back show through and are represented by broken lines, V.31908a, $\times 1000$.

A-C, F, Marske Quarry. D, E, Whitby.

Halle's specimen from Whitby consists of several closely associated fragments, only one of which had been figured; the whole group is now figured. All the fragments show very similar spikes, and traces of the annulus cells are to be seen in each. The artist's drawing of the fertile fragment (Thomas, 1912, pl. 4, fig. 2) is excellent, but the detailed drawing of the fertile spike (pl. 4, fig. 4) is a restoration based partly on a mistake; and this figure has been copied by others.

The specimen seems to have remained in an excellent state but neither I, nor others who have examined it, could see any more than what is shown in Text-fig. 48 D. (Broken lines mark the imprint where the substance has flaked off.) The spike appears to be slightly tilted, the bodies on the left are not sporangia and show no trace of annulus cells, but the pinnules are fertile. The annulus cells of two series of sporangia can be seen, one up the middle and one to the right, but the cells are much fewer than in Thomas' pl. 4, fig. 4 and the sporangia are not clearly marked but form only indistinct bulges with no definite boundary. All the other fertile spikes of this specimen were examined and each shows just two series of ill-marked sporangia, but never more.

A sporangium from this specimen was macerated and proved to contain a mass (perhaps 100) of spores which were poorly preserved and not separable for a count, probably being slightly unripe. Thomas' slide, which probably represents one sporangium, also contains about the same number of imperfectly separated spores. The spores are so like those of *Klukia exilis* that I suspected there might be contamination. As the same spores are found in the Whitby and Marske specimens, in neither of which locality does ordinary material of *Klukia* occur, this can be ruled out.

The spores in Thomas' preparation (figured here) are very lightly macerated and all about 45μ – 60μ wide. The spores isolated in preparing the transfer were larger (mean about 60μ , largest about 85μ) but their large size may be due to swelling in maceration. The spores in Halle's specimen are like those of Thomas' preparation but with thinner and less well-preserved walls. In all spores the reticulate markings on the back of the spore are so strong that it is difficult to see the much fainter tubercles on the facets.

AFFINITY. This must depend on the interpretation of the fertile spike. The facts here demonstrated are that the spike is dorsiventral, from above it shows a series of small scales (regarded as fertile pinnules) which continue the alternating sequence of sterile pinnules below the spike. From below it shows two series of sporangia only. These sporangia probably occur one below each fertile pinnule, but this is not proved. The outlines of the sporangia are very obscure indeed, unlike those of, say, *Klukia*, and the reason why they are so indistinct may be due to the presence over it of a protective membrane, much as in *Lygodium*. The sporangia and the fertile pinnules also seem to become smaller towards the apex of the spike. The sporangia remain attached after dehiscence. The spore output (around 100) is perhaps rather small, but may not represent one of the larger sporangia. The spores themselves are just like those of the Schizaeaceous affinity.

The only fact which speaks against it is the rather extensive annulus, though it must be remembered that as the shape of the sporangium is unknown, it is possible that the dehiscent sporangium may be open and show nearly its whole annulus when ten cells would not be too many for a Schizaeaceous fern. The final classification must, however, await effective study of the sporangium, and good balsam transfers should supply the information needed.

COMPARISON. 1. *Other species of Stachypteris.* The Yorkshire specimens of *S. hallei* Thomas are here united with *S. spicans*. The words of the diagnoses given by Thomas (1912) and by Saporta (1872) are different, but scarcely imply any specific difference, nor did Thomas state any difference. There is no general difference at all between the figures. Five other species of *Stachypteris* have been distinguished by name, one of which (*S. pulchra*) was synonymised in *S. spicans* by Saporta (1872). Saporta and Turutanova-Ketova give diagnostic

characters of the remaining species which are entirely unconvincing; they do not even apply to all the specimens they are supposed to cover. *Stachypteris inenarrabilis* Hollick (1930: 40, pl. 1, fig. 9), from the Cretaceous of Alaska, is a poorly characterised, sterile *Sphenopteris*.

2. *Other ferns*. No fossil resembles the fertile leaf of *Stachypteris* enough to be confused with it, but sterile leaves are so like a number of finely divided fern-like leaves of the Upper Jurassic and Lower Cretaceous that records of sterile leaves alone are valueless.

Thomas (1912) pointed out the resemblance of sterile leaves of *Stachypteris* to species of *Coniopteris*.

According to the treatment of *Coniopteris* in the present work *Stachypteris* most closely resembles fragments of the finely divided forms of *Coniopteris murrayana*. There is agreement in the size and shape of pinnae, pinnules, their katadromic branching and even in the enlarged size of the first acroscopic lobe of a pinnule. The solid rachis of *Stachypteris*, however, often serves to distinguish it from *C. murrayana* and the sori are entirely different.

As stated above, the spores are like those of *Klukia exilis*. In *Stachypteris* the facets may be less obviously tuberculate and the 'margo' or region next the triradiate crack is less thickened. The differences are so slight that it is scarcely possible to separate isolated spores of the two kinds.

Family DICKSONIACEAE

Both sections of this family, the Dicksonioideae and the Thyrsopteroideae occur fossil but their proportions are reversed. At present there is a single species in the Thyrsopteroideae and about forty in the Dicksonioideae; in the Yorkshire flora the Thyrsopteroideae have eight and the Dicksonioideae two. The facts on which this classification is based are however incomplete. In particular it is seldom possible to decide whether the annulus continues past the stalk in a crushed mass of sporangia.

Several species here included in the genus *Coniopteris* look very like such 'Polypodiaceous' genera as *Davallia* and *Odontosoria*. This is illustrated by Teixeira (1948) in his use of *Davallia* for a Cretaceous fern like *C. hymenophylloides* and the use of *Odontosorites* by Kobayashi & Yosida (1944) for a Jurassic fern like *C. burejensis*. *Davallia* is, however, well distinguished by its bilateral spores, but there is little to suggest whether the fossils are closer to *Thyrsopteris* or *Odontosoria*.

It is to be noted that Copeland merges the Dicksoniaceae in his Pterideae which avoids the difficulty of classification. Christensen's classification (to keep the Dicksoniaceae apart) is preferable, however, because this forces us to recognise our lack of essential knowledge of the fossils.

The Dicksoniaceae as treated here is the largest family of Yorkshire ferns and by far the commonest, *C. hymenophylloides* is especially abundant. It has also proved the most difficult to divide into species. This is shown, for example, by the chaotic labelling of Museum material. The spores were found to be disappointingly uniform, and transfer preparations were often not very helpful.

Much use has been made of the occurrence in the field; the different species being locally common, just like any other fossil, and had I been limited to unlocalised Museum material little could have been done. Use has also been made of a character previously neglected in Mesozoic ferns, the order of branching, see Text-fig. 51. It would appear that in many ferns

this order of branching is nearly constant; in others it is varied. In nearly all Recent British ferns, for example, the order is more or less strongly anadromic, in nearly all Palaeozoic ones it is strongly katadromic. It is not suggested that it should be used as an absolutely reliable character, which it is not, but merely as one of the more reliable ones for fern fragments. Nor do I wish to suggest an evolutionary transition from Text-fig. 51 A to 51 D through the intermediates, a subject on which I have no opinion.

The genera of the Dicksoniaceae are here arranged as follows:

Subfamily DICKSONIAE.

Indusium of 2 valves; only genus *Dicksonia sensu lato*.

Subfamily THYRSOPTERIDEAE.

Indusium a continuous cup (but possibly flattened and lobed).

Three fossil genera:

Coniopteris (= *Thyrsopteris*). Sterile pinnule Sphenopterid; fertile more or less reduced to a midrib and lateral sori; placenta nearly flat.

Kylikopteris gen. nov. (= *Coniopteris arguta*). Sterile pinnule Pecopterid; fertile strongly reduced to a terminal stalked sorus; placenta elongated.

Eboracia (= *E. lobifolia*). Sterile pinnule Pecopterid or Neuropterid; fertile only slightly reduced, sori marginal; placenta elongated.

Genus CONIOPTERIS Brongniart 1849: 26

1834 *Thyrsopteris* Kunze, p. 506.

1835 *Tympanophora* Lindley & Hutton, pl. 170.

1849 *Coniopteris* Brongniart, p. 26.

TYPE SPECIES—? *Coniopteris murrayana* (Brongniart), see below.

EMENDED DIAGNOSIS. Rachis smooth or hairy, never scaly. Frond two or more times pinnate. In sterile leaf or parts of leaf, pinnae divided into wedge-shaped pinnules or finely dissected. In fertile leaf or parts of leaf, fertile segments bearing sori marginally on the ends of lateral veins, or sorus appearing stalked. Sorus with a short placenta and a cup-shaped indusium, sometimes flattened in the plane of the lamina, or more or less divided into upper and lower lobes. Sporangia fairly small, rather wedge-shaped; annulus well developed, nearly vertical but probably complete. Stalk short and thick; spore output about 64; spores rounded tetrahedral with nearly smooth walls.

DISCUSSION. *Coniopteris* is most unsatisfactory in nomenclature. Brongniart founded it for the sterile leaf *Sphenopteris murrayana* and for what he regarded as its fertile leaf *Tympanophora racemosa* (which probably belongs to another species). He also included several Sphenopterid ferns only known in the sterile condition, some of considerably greater age. They include *S. athyrioides*, which may be *Todites princeps*. He did not, curiously enough, include *Sphenopteris hymenophylloides* and he gave no reason for replacing the earlier name *Tympanophora*. Subsequently *Coniopteris* was only used intermittently until Seward (1900) adopted it since when it has been in general use. It is employed here chiefly to avoid changing established names and because a general revision of these ferns is due and the change should be made then.

The familiar sori of *C. hymenophylloides* were taken as typical of the genus as little was known about the sori of *C. murrayana*, the type species. (The obscure fertile pinnules attri-

buted to it were in fact *Aspidistes*.) It now proves that the sori of *C. hymenophylloides* are like those of *Thyrsopteris* while the sori of *C. murrayana* are more like those of the living genera *Lindsaya*, *Odontosoria* and *Schizoloma*. *C. burejensis* also has sori rather like these three living genera. We still do not know whether the annulus continues past the stalk in most of the fossil species. Another living genus with sori like *Coniopteris* is *Davallia*, but this is clearly distinguished by the spores which are wedge shaped and not triradiate. I am indebted to Dr. R. A. Couper and to Dr. R. Holttum for advice on spores.

Key to sterile Yorkshire fragments of *Coniopteris*

- | | | | | | | | |
|--|---|---|---|---|---|-----------------------------------|---|
| (1) Pinna triangular (tapering from base to apex) | . | . | . | . | . | <i>C. murrayana</i> | |
| Pinna linear lanceolate, lower part scarcely tapered | . | . | . | . | . | . | 2 |
| (2) All segments filiform. 1 veined | . | . | . | . | . | <i>C. simplex</i> | |
| | | | | | | and probably <i>C. margaretae</i> | |
| Some or all segments broader with 2 or more veins | . | . | . | . | . | . | 3 |
| (3) Pinnules mostly divided less than half way to midrib | . | . | . | . | . | <i>C. burejensis</i> | |
| Pinnules mostly divided more than half way to midrib | . | . | . | . | . | . | 4 |
| (4) Apices of narrower segments rounded | . | . | . | . | . | <i>C. bella</i> | |
| Apices of narrower segments pointed | . | . | . | . | . | <i>C. hymenophylloides</i> | |

Coniopteris simplex (L. & H.) n. comb.

Text-figs. 49, 50 A-G

1. Yorkshire specimens.

- 1835 *Tympanophora simplex* Lindley & Hutton, p. 57, pl. 170 A. (Fertile pinna.)
 1835 *Tympanophora racemosa* Lindley & Hutton, p. 58, pl. 170 B. (Fertile pinna.)
 1900 *Coniopteris quinqueloba* (Phillips): Seward (in part), p. 113, text-figs. 14 A, B and 15 only. (Sterile and fertile pinnae. Pl. 16, fig. 8 is *C. hymenophylloides*.)
 1951 *Coniopteris tatungensis* Sze: Hare, p. 1140, text-figs. 1, 2. (Sterile, fertile, sporangia and spores, with a few figures not reproduced here.)

2. Specimens from other regions.

- ?1930 *Sphenopteris tyrmensis* Turutanova-Ketova, p. 141, pl. 1, figs. 7, 8. (Sterile pinnae. Kara-Tau, Central Asia.)
 1933 *Coniopteris tatungensis* Sze, p. 10, pl. 2, figs. 1-7. (Sterile and fertile. China.)

3. Similar leaves regarded as distinct though not separable by fully satisfactory characters.

- 1867 *Hymenophyllites leckenbyi* Zigno, p. 95, pl. 9, figs. 3-5; pl. 14, fig. 1. (Upper Lias; Italy.)
 1872 *Stachypteris* spp. (sterile only), Saporta. (Upper Jurassic; France.)
 1913 *Sphenopteris leckenbyi* (Zigno): Halle, p. 31, pl. 3, figs. 20, 20a. (Middle Jurassic; Graham Land.)
 1937 *Coniopteris angustiloba* Brick (see Brick, 1937, where earlier references are given). This was held to be the same as *C. tatungensis* Sze but it appears to differ in branching at a smaller angle and in having coarser lobes. Central Asia.

EMENDED DIAGNOSIS. Leaf as a whole lanceolate or linear lanceolate, width about 8 cm., length unknown, apex acute, base unknown. Rachis typically 2 mm. wide, grooved above, rounded below.

In sterile leaf, pinnae arising at about 70° and at intervals of about 1 cm., very easily detached. Pinna rachis very slender, grooved above, basal secondary branches opposite, others becoming alternate in katadromic order. Secondary branches equal on the two sides, typically 5 mm. long, very gradually reduced towards the pinna apex; lowest secondary branches unspecialised, not overlapping the rachis. Tertiary branches usually opposite and arising at right angles to the secondary.



Fig. 49. *Coniopteris simplex* (L. & H.)

A, leaf apex, V.29231, $\times 1$. B, isolated pinna with rather thick branches, V.29230, $\times 2$. C, fertile pinna, V.32021, $\times 2$. D, details of part of C, $\times 4$. E, fertile pinna, V.32022, $\times 2$. F, exceptionally large fertile pinna, V.29232, $\times 2$. G, middle part of lamina, Leckenby Coll., 351, Sedgwick Museum, Cambridge, $\times 1$. H, sterile pinna with thin branches, $\times 2$. I, partly fertile pinnae with thin branches, V.32023, $\times 2$. J, details of part of I, $\times 8$. A, B, F, are from Hare (1951, text-figs. 1, 2) and represent specimens from Cloughton *quingueloba* Bed. G, unlocalised (? Haiburn). All the others are from Haiburn Wyke *Zamites* Bed.

Fertile leaf not known as a whole; fertile pinnae often longer than sterile; usually including some or many sterile segments, the sorus tending to be on the acroscopic and the sterile segments on the basiscopic side. Sori stalked, borne singly in the distal part of the pinna but in opposite pairs on secondary branches below. Fertile pinnule and sorus stalk very slender. Indusium cup shaped, up to 1.5 mm. wide (often smaller), placenta low, sporangia probably shortly stalked, all of about the same age in a sorus; annulus composed of about 25–30 cells. Indusial cup composed of thick tissue below, but reduced near the margin to a delicate membrane; no external hairs present.

Spores rounded triangular, cuticle fairly thin, smooth; mean diameter 53μ (σ 6μ , range noted 37μ – 60μ ; occasional shrivelled spores down to 20μ not included in mean or σ). Tri-radiate marks clear but not prominent, bordered by a slightly thickened margin.

DISTRIBUTION. *C. simplex* is rather common but the sterile leaf is so finely divided it is often difficult to see. The sori of fertile fragments make them more conspicuous and, so, apparently commoner than the sterile fragments. Its localities are as follows:

Middle Deltaic Gristhorpe Series:

Cloughton Wyke '*quineloba* Bed' (abundant, sterile and fertile).

Fryup Dale Coalpits (rare, sterile).

Farndale Harland Park Coalpits (rare, sterile).

Middle Deltaic Sycarham Series:

Haiburn Wyke, *Equisetum* Bed, just above the Iron Scar (sterile and fertile).

Lower Deltaic Series:

Saltwick, nr. Waterfall (sterile).

Hawsker, Jack Ass Trod, *Nilssonina* Bed (sterile and fertile).

Hawsker, Maw Wyke, fallen block (sterile and fertile).

Beast Cliff, fallen blocks of '*C. tatungensis*' Bed (abundant, sterile and fertile).

Haiburn Wyke, *Zamites* Bed (abundant, sterile and fertile, but mixed with other ferns).

The Leckenby specimen K.351 is only localised as 'Inferior Oolite, Yorkshire'.

DISCUSSION. Text-fig. 49 G shows some of the middle part of a sterile leaf; the best specimen figured by Hare (1951) being a leaf apex. The main rachis of this specimen is slightly hairy and this helps to identify certain associated axes, 2–4 mm. wide, as petioles. No other recognisable fossil occurs in this block. (Hare noticed the association of similar petioles with her material where also no other recognisable fossil occurred). If, as seems likely, these are true petioles the whole leaf must be of moderate size only and the specimen figured represents the main rachis and its branches and not merely a pinna.

Wherever this species occurs commonly the pinnae are found detached, though normally undamaged. They must have broken off very easily.

Fertile pinnae are remarkably common, nearly half as common as the sterile and are known from all localities where there is good sterile material. The presence of characteristic sterile segments among the fertile pinnae serves to identify them. The sori appear to have been tilted

slightly out of the plane of the leaf as a whole (perhaps downwards) and favourable transfers show that the indusium is a complete cup (though not necessarily a round one) and that the placenta is a low bulge.

In most fertile specimens nearly all sporangia have been shed but it is generally possible to obtain a few spores from them. The bedding plane of some of these specimens is covered with empty, stalkless sporangia which may well belong to this species. The specimen shown in

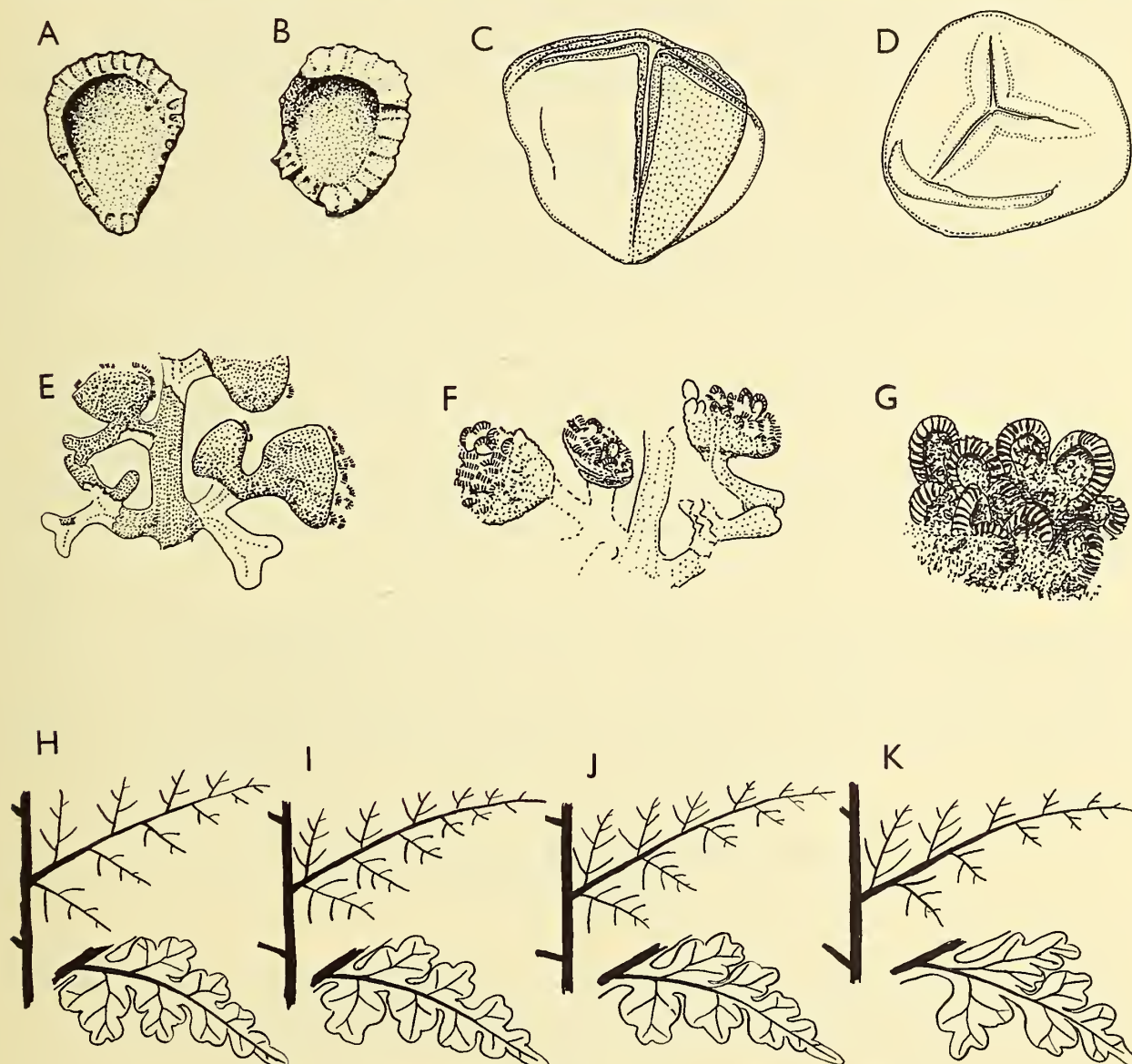


Fig. 50. *Coniopteris simplex* (L. & H.); Generalised diagrams

A, B, isolated empty sporangia associated with *C. simplex*, V.29233-34, $\times 75$. C, D, two spores from E, $\times 800$. E, fertile fragment with its sporangia, V.40256, $\times 10$. F, same fertile fragment as a balsam transfer, $\times 10$. G, sporangia from F, $\times 40$.

H-K, diagrams representing four styles of branching in pinnate fern leaves. H, strongly katadromic. I, opposite becoming katadromic. J, opposite becoming anadromic. K, strongly anadromic. See pp. 96, 141. A, B, from Cloughton *quineloba* Bed. After Hare (1951, text-fig. 2 B, C). C-G, Haiburn *Zamites* Bed.

Text-fig. 50 E, however, retains its sporangia. The sori are slightly tilted and the sporangia are only well seen in transfer. This specimen shows that the one figured by Seward (1900, text-fig. 15) does belong to *C. simplex*. This, as Hare pointed out, appears to show almost no indusium, but no doubt because it is tilted. It is still not possible to say whether the annulus continues past the stalk, but it is clearly almost vertical and the stalk is rather thick. It was not possible to obtain a reliable spore count as intact sporangia could not be isolated, but there is some evidence that the number is less than 100 but over 50.

IDENTIFICATION. The present material is identical with the fertile fragments described by Lindley & Hutton as *Tympanophora simplex*, and no doubt also with their *T. racemosa*, though it is not quite so characteristic. Compare, for example, Text-fig. 49 C, D, E with Lindley & Hutton's figure. *T. simplex* and *T. racemosa* had been regarded as the fertile pinnae of *C. hymenophylloides* but I am now convinced that the fertile pinna of *C. hymenophylloides* is normally distinguished by a stouter stalk to its sorus and any sterile segments also are broader. It may be noticed that Lindley & Hutton's specimens were collected at Cloughton, but it is not known whether they came from the same bed as Hare's material. The Yorkshire material is just like that from Shensi, China. Sze (1933a) regards this flora as Liassic rather than Oolitic, but the associated species look very similar and there may be little difference of age.

COMPARISON. This species has been confused with Phillips' *Sphenopteris quinqueloba* which I believe to be a slender form of *Coniopteris hymenophylloides*. Phillips' sketch of '*S. quinqueloba*' shows a very narrow pinna with rounded ultimate ramuli, very different from the broader pinna with spreading, filiform, ultimate ramuli of the present fern. It was as a result of this confusion that the first locality in which I found it at Cloughton was called the '*quinqueloba* bed'.

Since 1900 fertile pinnae of *C. simplex* have been attributed to *C. hymenophylloides*. Differences are in *C. simplex* the pinnule is very slender; in *C. hymenophylloides* it is usually broad enough to show lateral veins. In *C. simplex* towards the end of the pinna and often elsewhere there is a filiform sterile segment below each sorus; in *C. hymenophylloides* any sterile tissue which may exist here forms a very short, broad lobe. The spores of *C. simplex* are distinctly larger, mean 53μ as against 40μ , and this is not a result of different times of maceration.

Coniopteris burejensis (Zalessky) Seward

Text-fig. 51 E-M

Specimens from E. Asia and other regions.

- 1876a *Thyrsopteris Maakiana* Heer, p. 31, pl. 1, figs. 1-3; pl. 2, fig. 6. (Sterile fragments only considered. Siberia.)
- ?1876a *Thyrsopteris Murrayana* Heer, p. 30, pl. 2, figs. 2, 3. (Sterile fragments. Siberia.)
- ?1876a *Dicksonia concinna* Heer, pp. 34, 87; pl. 16, figs. 1-7. (Sterile and fertile. Siberia and Amurland.)
- ?1876a *Dicksonia saportana* Heer, p. 89, pl. 17, figs. 1, 2; pl. 18, figs. 1-3. (Sterile and fertile. Amurland.)
- ?1876a *Adiantites nympharum* Heer, p. 93, pl. 17, fig. 5. (Sterile. Amurland.)
- ?1876a *Adiantites amurensis* Heer, p. 94, pl. 21, fig. 6a, b. (Sterile fragments. Amurland.)
- ?1878 *Dicksonia borealis* Heer, p. 14, pl. 3, figs. 15-17. (Sterile fragments. Siberia.)
- 1904 *Dicksonia Burejensis* Zalessky, pp. 181, 192, pl. 3, figs. 1-4; pl. 4, figs. 1-5; text-fig. 1. (Sterile leaves and fertile fragments. Amurland.)
- 1912 *Coniopteris burejensis* (Zalessky) Seward, pp. 6, 22, pl. 1, figs. 1-5; pl. 3, figs. 18-21. (Sterile leaves; fertile pinnae. Amurland.)
- 1912 *Coniopteris burejensis* (Zalessky): Novopokrowski, p. 5, pl. 1, fig. 6, 6a; pl. 2, figs. 4, 6, 6a. (Good sterile and fertile fragments. Amurland.)

- ?1914 *Coniopteris burejensis* (Zalessky): Knowlton, p. 46, pl. 5, fig. 1. (Part of a very large fertile leaf. Alaska.)
 1915 *Coniopteris burejensis* (Zalessky): Kryshstofovich, p. 85, pl. 1, fig. 5; pl. 2, figs. 1-8; pl. 3, figs. 1-2; text-figs. 1-5. (Good sterile and fertile specimens. Amurland.)
 ?1928 *Coniopteris burejensis* (Zalessky): Yabe & Oishi, p. 8, pl. 2, fig. 11. (Sterile fragment. China.)
 ?1930 *Coniopteris burejensis* (Zalessky): Turutanova-Ketova, p. 136, pl. 1, fig. 10. (Sterile fragment. Central Asia.)
 1931 *Coniopteris burejensis* (Zalessky): Sze, p. 43, pl. 7, figs. 5-8. (Sterile and fertile fragments. Lias; China. Comparison with *C. hymenophylloides*.)
 1938 *Coniopteris burejensis* (Zalessky): Oishi & Takahasi, p. 59, pl. 5, figs. 3, 3a, 3b, 4. (Sterile and fertile fragments. Middle Jurassic; Manchuria.)
 1940 *Coniopteris burejensis* (Zalessky): Oishi, p. 206, pl. 3, fig. 4; pl. 4, figs. 1-4. (Sterile and fertile leaves. Japan.)
 ?1944 *Odontosorites heerianus* (Yokoyama): Kobayashi & Yosida, p. 257, pl. 28, figs. 6, 7; text-fig. A-C. (Sterile and fertile leaves. Manchuria.)

DIAGNOSIS. (Leaf as a whole unknown, but probably very large and typically three times pinnate, largest leaves almost four times pinnate.) Primary pinna long, lanceolate, upper part tapering gradually. Rachis up to 4 mm. thick. Secondary pinnae rather crowded and overlapping, length typically 12 cm. but often more. Secondary pinna typically uniformly about 10 mm. wide in proximal half, tapering gradually in distal half. First pinnule arising near the pinna rachis on the basiscopic side, later pinnules alternating katadromically. Pinnules on the two sides equal, basal ones unspecialised.

In typical sized leaf, sterile pinnule rhomboidal, about 7 mm. \times 2.5 mm., apices acute, pointing forwards; margins more or less indented to form lobes with sharp apices. In large leaf, pinnules elongated, up to 15 mm. long, margins deeply divided into numerous forward pointing acute lobes. Midrib nearer basiscopic margin at base of pinnule (first acroscopic lobe being larger than first basiscopic). Midrib strong, giving off veins at a small angle, lower veins opposite, upper ones tending to alternate katadromically. Lamina flat, fairly thick, smooth and hairless.

Fertile leaf probably like sterile, partly fertile pinnae very frequent. Fertile pinnules typically longer and narrower than sterile, sori borne singly on lower lateral lobes and pointing forwards; upper lobes often remaining sterile. Lamina typically not contracted below a sorus, lamina often continuing as a narrow wing along the outside of a sorus. Sorus with a vein supplying the placenta and often a branch to the lamina at its side.

Placenta nearly flat, sporangia stalked, annulus well developed about 250 μ wide. Indusium (possibly) flattened but continuous at the sides, fairly robust and similar in texture to lamina; margin entire. Spore rounded triangular, about 40 μ wide, walls moderately thick, almost smooth (or very finely granular). Triradiate crack with an ill-defined but slightly thickened margin.

DISTRIBUTION. *Coniopteris burejensis* is widespread in rocks of Middle Jurassic age in temperate E. Asia, and occurs in Central Asia, and probably Alaska, but this is the only record from Europe. It is rare in Yorkshire, being confined to a single Lower Deltaic locality (Beast Cliff, Fern Bed) where, however, fragments are numerous and unmixed with other species.

DISCUSSION. No attempt has been made to alter the name of this fern, but possibly one of Heer's numerous species has priority. His material deserves re-examination.

Zalessky considered that his larger specimens might represent pinnae rather than whole leaves. It is fairly certain that some specimens at least represent very large leaves (e.g. Seward 1912, pl. 3, fig. 20; Knowlton, 1914, pl. 5, fig. 1), the others may be isolated pinnae, or just

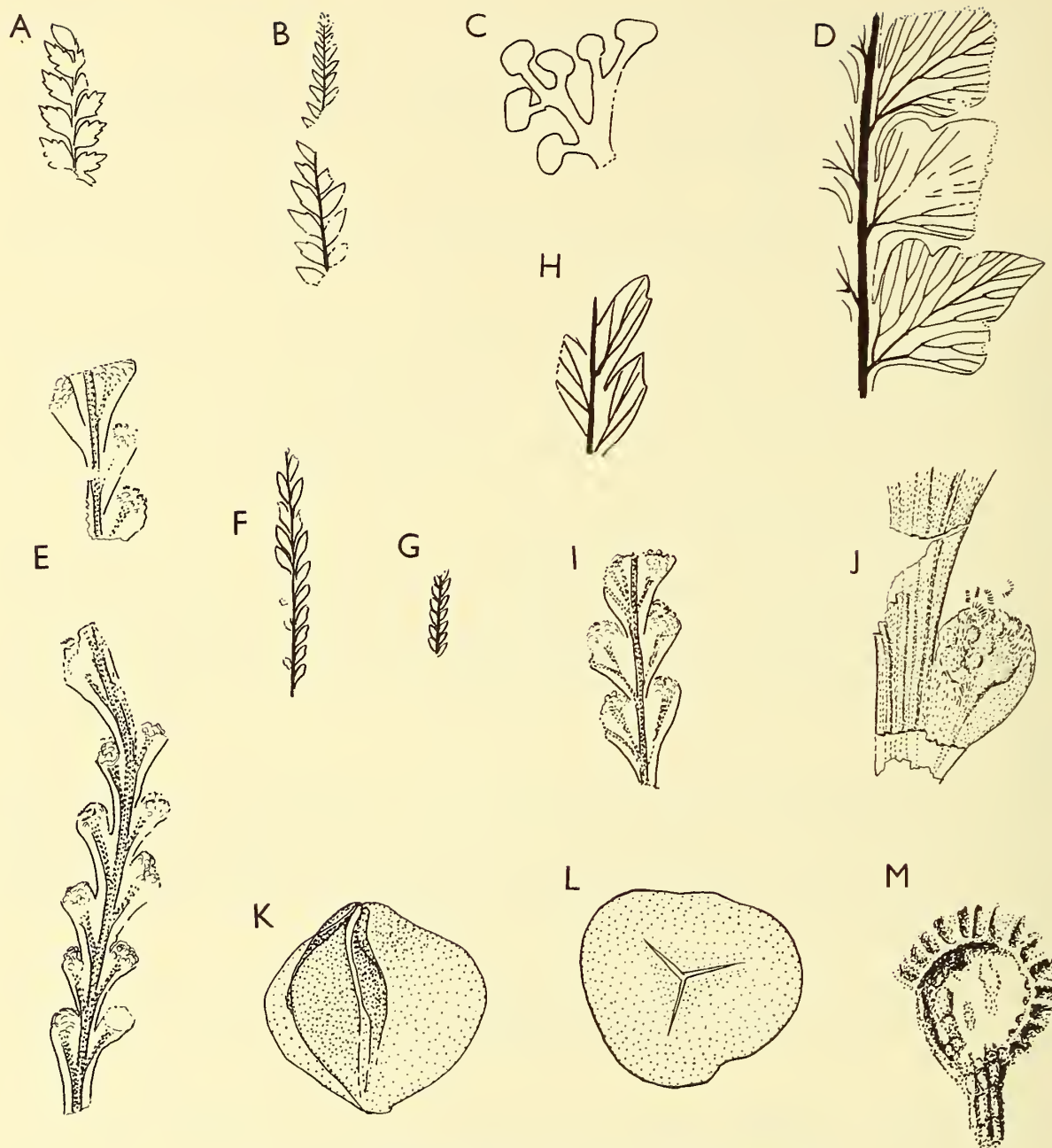


Fig. 51. *Coniopteris bella* sp. nov., *C. burejensis* (Zalessky)

A-D, *C. bella*. A, typical pinna fragment, V.32001, $\times 1$. B, pinna apex, V.32003, $\times 1$. C, associated fertile fragment, V.32005, $\times 4$. D, pinnules, V.32002, $\times 4$.

E-M, *C. burejensis*. E, fertile fragment, the gap is caused by a break in the rock, V.32004, $\times 4$. F, G, typical sterile fragments, V.31996, $\times 1$. H, venation of sterile fragment, V.31997, $\times 4$. I, fertile fragment, note the outer veins on the left, V.31998, $\times 4$. J, details of part of E, $\times 12$. K, L, spores from E, $\times 800$. M, detached sporangium, V.31999, $\times 100$.

A, D, Burniston *Zamites* Bed. B, C, Moss Gill. E-M, Beast Cliff Fern Bed.

rather small leaves. The present small fragments throw no light on the form of the whole leaf, but they agree perfectly with various Asiatic fragments and provide some new information about the sorus.

COMPARISON. *C. burejensis* pinnules are often very like those of *C. bella*, and, indeed, hardly to be distinguished from figured specimens. The lobe apices in *C. burejensis* are, however, usually angular and often acute, whereas in *C. bella* they are rounded or at most obtuse. The lamina is also more delicate in *C. bella*. The sori are more different, being usually borne on a 'stalk' in *C. bella* and never accompanied by a marginal wing of lamina. The indusium is much more delicate in *C. bella*.

The following characters (partly taken from Sze, 1931) distinguish *C. burejensis* from *C. hymenophylloides*. The sterile leaf never shows aphlebioid basal pinnules; the pinnules vary from rhomboidal to dentate-linear with acute lobes, rarely obtuse lobes; the fertile leaf often shows partly fertile, partly sterile pinnules, the fertile pinnules often have a broad lamina with almost sessile sori, or sori bearing a wing of lamina on the outer side. The lamina is rarely contacted under a sorus to form a stalk. It is thought also that the leaf of *C. burejensis* is much larger, and also that the indusium is much more flattened.

Coniopteris bella sp. nov.

Text-figs. 51 A-D, 52

1864 *Tympanophora simplex et racemosa* Leckenby (non L. & H.), p. 79, pl. 11, fig. 2. (Apex of partly fertile leaf.)

1917 *Coniopteris hymenophylloides* Brongn.: Seward, text-fig. 272, on p. 369. (Partly fertile leaf here refigured in Text-fig. 52.)

DIAGNOSIS. Leaf fairly large, long-lanceolate, bipinnate to tripinnate. Rachis up to 3 mm. thick. Pinnae rather crowded and overlapping, typically about 7 cm. long in the middle of the leaf and making an angle of 70°–80° to the rachis. Primary pinna typically about 10 mm. wide at the base, tapering very gradually to the apex. Basal pinnules often opposite, later ones tending to alternate katadromically. First pinnule on the basiscopic side showing small aphlebiform lobes near the rachis (but these often hidden). Pinnules ovate to rhomboidal, length up to twice their width, shape never linear; larger ones divided halfway or more into rounded lobes, or subdivided into one-veined segments, about 0.7 mm. wide; apices of lobes or segments rounded, rarely obtuse, never acute. Branches of pinnules irregular, basal lobes typically opposite, later lobes opposite or alternating anadromically or katadromically. Lamina flat, hairless; substance very delicate but more than one cell thick.

Fertile leaf resembling sterile and most specimens partly fertile, at least in upper parts; sterile and fertile pinnules showing a complete inter-gradation. Fertile pinnules shaped as in sterile, typically showing a sorus at the end of each filiform segment or two sori on the margin of a compound lobe. Sorus typically wider than the segment bearing it (and therefore appearing stalked). Placenta flat, surrounded by an indusium extending considerably beyond the sporangia. Indusium in lateral view rounded or slightly longer than broad, never widely open. Free end of the indusium divided into an upper and lower lobe with an entire more or less rounded margin; substance membranous, very delicate, formed of a single layer of elongated cells.

Sporangia shortly stalked, rather small (up to 200 μ wide), annulus well developed; containing about 64 spores. Spores rounded triangular, mean size about 40 μ (range noted 32 μ –

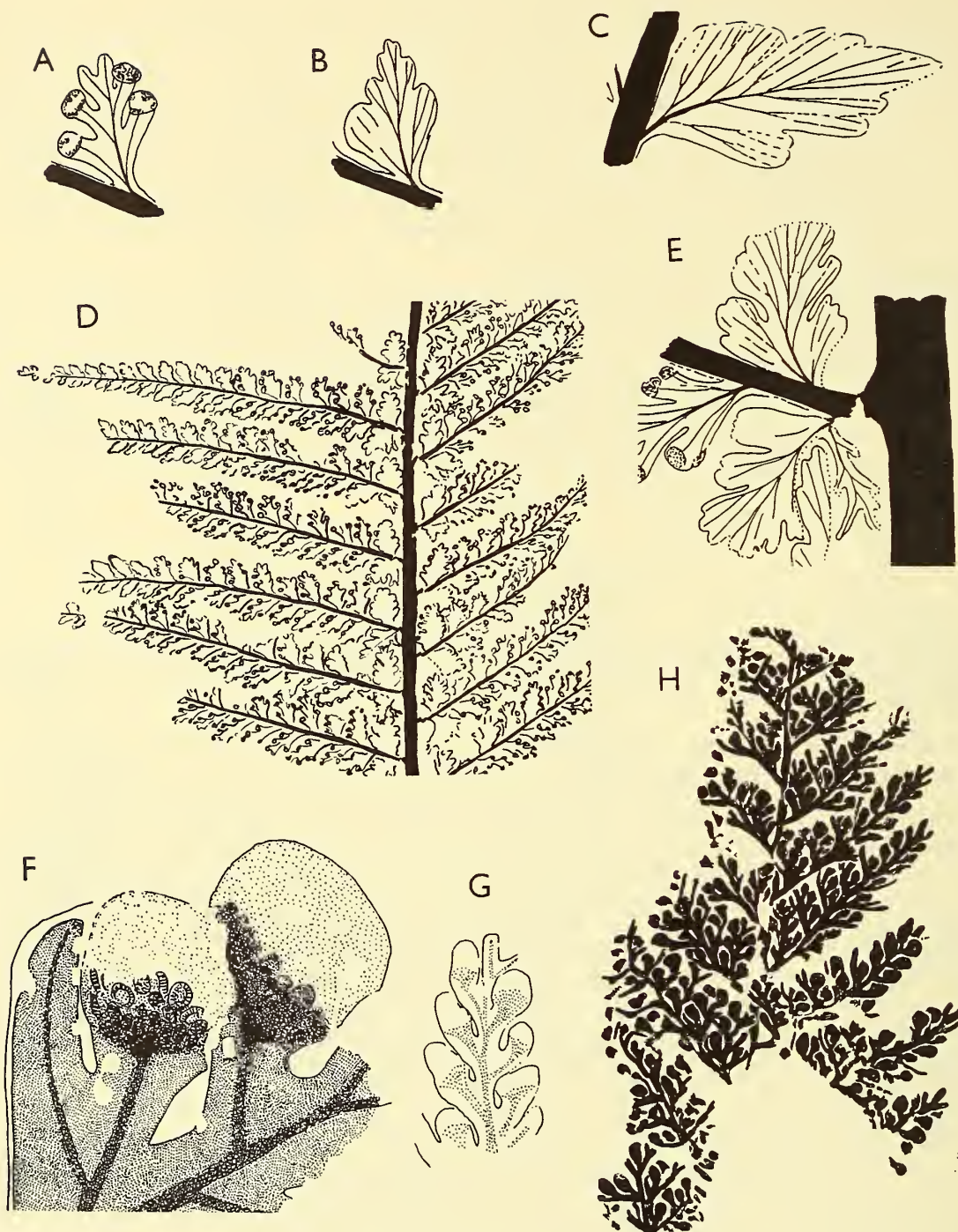


Fig. 52. *Coniopteris bella* sp. nov.

A, B, pinnules from near the middle of a pinna of D, $\times 4$. C, pinnule of an associated sterile pinna, $\times 4$. D, about two-thirds of the principal specimen, $\times 1$. E, basal pinnules from D, the aphlebiform process is only seen because part of an overlapping pinnule is broken away, $\times 4$. Specimen also figured Seward (1917, text-fig. 272). A-E, from a slab of reddish sandstone in Yorkshire Museum labelled '*Sphenopteris stipitata*' and 'Upper Shale and Sandstone, Scarbro'. F, two sori from H, $\times 20$. G, pinna from H, $\times 5$. H, specimen, V.28474 from Gristhorpe Bed.

50 μ) walls moderately thick, very nearly smooth. Triradiate crack well-marked, margin slightly thickened but ill-defined.

DISTRIBUTION. *C. bella* is fairly widespread, especially in the Upper Deltaic in Yorkshire, but has been confused with *C. hymenophylloides*. It is known from the following localities:

Upper Deltaic:

Jugger Howe: Moss Gill Slack (numerous sterile and fertile fragments).
Burniston Wyke, Black's Bed B. (rare sterile and fertile fragments).
Scalby Ness, *Ginkgo* Bed (rare sterile fragments).
Burniston *Zamites* Bed (sterile and fertile fragments).

Middle Deltaic Gristhorpe Series:

Gristhorpe Bed (sterile and fertile leaves).

Lower Deltaic:

Fallen blocks at High Whitby Fog Signal (sterile and fertile fragments).

It is also represented by a series of imperfectly localised but large specimens in museums preserved in fine grained sandstone. The matrix is unfamiliar and may represent one or more quarries now closed.

C. bella is not yet known outside Yorkshire, but it may well be that the study of fertile material would show it occurs elsewhere; indeed some of the specimens attributed to *C. burejensis* or to *C. hymenophylloides* could almost equally well belong to it.

DISCUSSION. The sorus of *C. bella* is interesting since the indusium is partly divided into upper and lower lobes, but the division does not seem to extend to the base. It is only the Gristhorpe specimen which is well enough preserved to show this, but here it seems certain as the lateral margins are seen separately in the apical parts of several sori.

Spores were prepared from all fertile specimens; they proved uniform. Specimen no. 60/2462 in the Yorkshire Museum gave on gentle maceration what appeared to be spore masses of separate sporangia. These, when separated, yielded 57, 66, 72 spores, and 64 is taken as the typical spore number.

The delicate lamina and nature of the sorus raised the question whether this fern might belong to *Hymenophyllum*. However, the lamina in the well-preserved Gristhorpe specimen shows more than a single set of cells, whereas the indusium shows a single set clearly. (It may be pointed out that none of the Mesozoic ferns attributed to *Hymenophyllum* has yet been proved to agree with it in structure.)

COMPARISON. *C. bella* differs from *C. hymenophylloides* as follows: The leaf is rather wider (length of pinnae usually more than 7 cm. instead of less) and the pinnae are more crowded so that the pinnules overlap. The basal aphlebiform lobes are smaller (usually less clearly seen) and the pinnules are often rhomboidal, reaching the full width near the middle, while in *C. hymenophylloides* they reach their full width almost at the base. The narrower lobes have rounded apices in *C. bella*, but obtusely or acutely angular apices in *C. hymenophylloides*. The texture of the lamina appears to be more delicate in *C. bella*.

The fertile leaf in *C. bella* usually or always has partly sterile pinnules, whereas this is exceptional in *C. hymenophylloides*. Fertile pinnules in *C. bella* are much less reduced and normally almost as wide as the sterile. The indusium is more delicate and much narrower, and divided into two lobes apically, instead of being a rather flattened but wide cup. The sporangia and spores are similar.

Coniopteris hymenophylloides (Brongniart) Seward

Text-figs. 53, 54

1. Yorkshire specimens.

- ?1829 'A skeletonized fern branch', Phillips, p. 190, pl. 8, fig. 18. (Poor figure.)
 ?1829 *Sphaenopteris stipata* Phillips, p. 153, pl. 10, fig. 8. (Poor specimen later regarded as *S. hymenophylloides*.)
 ?1829 *Sphaenopteris muscoides* Phillips, p. 153, pl. 10, fig. 10. (Figure useless, but specimen (at York) probably is *C. hymenophylloides*.)
 1829 *Sphenopteris hymenophylloides* Brongniart, p. 189, pl. 56, fig. 4. (Good sterile specimen.)
 ?1829 *Sphenopteris crenulata* Brongniart, p. 187, pl. 56, fig. 3. (Sterile fragments.)
 1835 *Sphenopteris arguta* Lindley & Hutton, p. 53, pl. 168. (Sterile pinna.)
 1851 *Sphenopteris nephrocarpa* Bunbury, p. 179, pl. 12, fig. 1a, b. (Good fertile pinnules.)
 1875 *Sphenopteris hymenophylloides* Brongn.: Phillips, p. 215, lign. 34, pl. 10, fig. 8. (Sterile and fertile.)
 1875 *Sphenopteris socialis* Phillips, p. 214, lign. 31.
 1875 *Sphenopteris quinqueloba* Phillips, p. 215, lign. 33.
 1875 *Sphenopteris crenulata* Brongn.: Phillips, p. 216, lign. 35.
 1875 *Sphenopteris denticulata* Brongn.: Phillips, p. 217, lign. 38, 39.
 1900 *Coniopteris hymenophylloides* (Brongn.) Seward, p. 99 (in part), pl. 16, figs. 4-6; pl. 17, figs. 6?, 7, 8?; pl. 20, figs. 1, 2; pl. 21, figs. 1-4. (Sterile and fertile.)
 1900 *Coniopteris quinqueloba* (Phillips): Seward, p. 112, pl. 16, fig. 8 only.
 1900b *Coniopteris hymenophylloides* (Brongn.): Seward, p. 5, fig. 1. (Sterile pinna.)
 1912 *Coniopteris hymenophylloides* (Brongn.): Thomas, p. 384, pl. 3, figs. 1-3. (Fertile fragment, sporangia.)

2. Specimens from other regions.

- 1863 *Sphenopteris Bunburyanus* Oldham & Morris, p. 54, pl. 32, figs. 5-7. (Sterile and fertile fragments, possibly this species. India.)
 ?1872 *Sphenopteris Pellati* Saporta, p. 278, pl. 31, fig. 1. (Sterile. Kimmeridgian; France.)
 ?1872 *Coniopteris conferta* Saporta, p. 289, pl. 31, fig. 3. (Fertile. Corallian; France.)
 1877 *Sphenopteris orientalis* Newberry, p. 122, pl. 9, fig. 1, 1a. (Large sterile leaf. China.)
 1877 *Hymenophyllites tenellus* Newberry, p. 122, pl. 9, fig. 4. (Fertile fragment. China.)
 1880 *Thyrsopteris orientalis* (Newb.): Romanowski, p. 130, pl. 28, fig. 1a-d. (Good sterile leaf. Tianshan, Central Asia.)
 ?1889 *Dicksonia nephrocarpa* (Bunb.): Yokoyama, p. 25, pl. 1, fig. 1, 1a. (Sterile and fertile fragments possibly this species. Japan.)
 1894 *Thyrsopteris murrayana* (Brongn.): Raciborski, p. 130, pl. 10, figs. 15, 16; pl. 12, figs. 17-20 (? not 21). (Sterile and fertile. Upper Lias; Poland.)
 1894 *Dicksonia Heerii* Raciborski, p. 174, pl. 10, figs. 5-14 (in part), pl. 12, figs. 8-12 only. (Similar fertile fragments but sterile different.)
 1906 *Coniopteris hymenophylloides* (Brongn.): Yokoyama, pp. 24, 26, pl. 6, fig. 3; pl. 7, figs. 1-5. (Sterile leaves and fragments. China.)
 ?1907 *Coniopteris hymenophylloides* (Brongn.): Seward, p. 21, pl. 6, fig. 48; pl. 7, figs. 51, 52. (Sterile and fertile fragments. Caucasus region.)
 1911 *Coniopteris hymenophylloides* (Brongn.): Seward, pp. 10, 38, pl. 1, figs. 11-13, ? 14, 15; pl. 6, figs. 67, 68. (Good sterile pinnae. Central Asia.)
 1911 *Coniopteris quinqueloba* (Phillips): Seward, pp. 11, 40, pl. 2, fig. 17, 17a, 17b. (Sterile pinna as above.)
 1911a *Coniopteris hymenophylloides* (Brongn.): Thomas, p. 385, pl. 3, figs. 4, 5. (Spores. Kamenka, Russia.)
 1911a *Coniopteris hymenophylloides* (Brongn.): Seward, p. 666, pl. 3, figs. 44-46a; pl. 8, fig. 27. (Jurassic; N. Scotland.)
 1911 *Coniopteris hymenophylloides* (Brongn.): Thomas, p. 62, pl. 2, figs. 3-9; pl. 8, figs. 7-10. (Good sterile and fertile pinnae, spores. Kamenka, Russia.)
 1912 *Coniopteris hymenophylloides* (Brongn.): Seward, p. 12, pl. 2, figs. 22-25a; pl. 7, fig. 87a. (Sterile and fertile fragments. Afghanistan.)
 ?1913 *Coniopteris hymenophylloides* (Brongn.): Halle, p. 19, pl. 3, figs. 23, 24, 27a, 28-30. (Sterile and fertile pinnae very short. Graham Land.)
 ?1914 *Coniopteris hymenophylloides* (Brongn.): Knowlton, p. 47, pl. 5, fig. 2. (Sterile fragments with coarse segments. Alaska.)

- 1917 *Coniopteris hymenophylloides* (Brongn.): Arber, p. 32, pl. 2, figs. 1-3, 6; pl. 3, figs. 3-5. (Sterile and fertile fragments. New Zealand.)
- 1925 *Coniopteris hymenophylloides* (Brongn.): Teilhard de Chardin & Fritel, p. 537, pl. 33, fig. 3a. (China.)
- ?1926 *Coniopteris hymenophylloides* (Brongn.): Kawasaki, p. 14, pl. 4, fig. 13. (Ill-preserved sterile fragment. Korea.)
- 1928 *Coniopteris hymenophylloides* (Brongn.): Yabe & Oishi (in part), p. 6, pl. 1, fig. 5 only. (Sterile. Shantung.) Pl. 2, figs. 1-10, sterile and fertile are more like *C. murrayana*.
- 1929 *Coniopteris hymenophylloides* (Brongn.): Yabe & Oishi, p. 103, pl. 21, figs. 1, 2, 2a. (Fertile fragments, Shantung.)
- 1930 *Coniopteris hymenophylloides* (Brongn.): Turutanova-Ketova, p. 135, pl. 1, fig. 9. (Sterile pinna. Tianshan, Central Asia.)
- 1931 *Coniopteris* cf. *hymenophylloides* (Brongn.): Prinada, p. 17, pl. 1, figs. 6, 7; text-fig. 2. (Sterile fragments, venation. Central Asia.)
- ?1931 *Coniopteris hymenophylloides* (Brongn.): Sze, pp. 34, 35, pl. 5, fig. 1. (Sterile leaves approaching *C. burejensis*. China. Comparison with *C. burejensis*.)
- 1933 *Coniopteris hymenophylloides* (Brongn.): Sze, pp. 11, 27, pl. 1, figs. 1-11. (China.)
- ?1933b *Coniopteris hymenophylloides* (Brongn.): Sze, p. 69, pl. 8, figs. 4, 5 only (? = *C. burejensis*. Kansu, China.)
- 1933c *Coniopteris hymenophylloides* (Brongn.): Sze, p. 78, pl. 11, figs. 1-3. (Sterile. Shensi, China.)
- 1933c *Coniopteris* sp. (? n. sp.) Sze, p. 79, pl. 11, figs. 4-13, 18, 19. (Sterile and fertile, spores. Shensi, China.)
- 1933 *Coniopteris hymenophylloides* (Brongn.): Prinada, p. 8, pl. 1, fig. 9, 9a. (Sterile fragment. Transcaucasia.)
- 1933 *Coniopteris hymenophylloides* (Brongn.): Yabe & Oishi, p. 210, pl. 30, figs. 13, 13a, 16-18; pl. 31, fig. 6; pl. 35, figs. 1, 7. (Sterile. Manchuria.)
- 1934 *Coniopteris hymenophylloides* (Brongn.): Edwards, p. 92, text-fig. 2. (Spores. New Zealand.)
- 1937 *Coniopteris hymenophylloides* (Brongn.): Brick, p. 15, pl. 3, figs. 1-5; pl. 4, fig. 1?, 2-4; pl. 5, fig. 1?; pl. 9 fig. 2?; text-fig. 6a-f. (Sterile and fertile leaves. Ferghana, see p. 158.)
- 1938 *Coniopteris hymenophylloides* (Brongn.): Oishi & Takahasi, p. 58, pl. 5, figs. 1, 1a, 2. (Manchoukuo.)
- ?1939 *Coniopteris hymenophylloides* (Brongn.): Kawasaki, p. 22, pl. 2, fig. 11. (Ill-preserved, sterile. Korea.)
- 1940 *Coniopteris hymenophylloides* (Brongn.): Sitholey, p. 10, pl. 2, fig. 33; pl. 3, figs. 34, 35. (Sterile and fertile fragments. Afghanistan; also perhaps *Sphenopteris* sp. on p. 10.)
- 1940 *Coniopteris hymenophylloides* (Brongn.): Oishi, p. 209. (List of Japanese localities.)
- ?1945 *Davallia alfeizeranensis* Teixeira, p. 1, pls. 1-3. (Good sterile and fertile pinnae. Lower Cretaceous; Portugal. See p. 158.)
- ?1948 *Davallia delgadoi* (Sap.) Teixeira, p. 27, pl. 12, figs. 1-11; pl. 13, figs. 1-6. (Figures mostly as in 1945.)
- 1949 *Coniopteris hymenophylloides* (Brongn.): Sze, p. 7, pl. 13, figs. 3-7; pl. 14, figs. 4, 5. (Sterile pinnae. Hupeh, China.)
- 1952 *Coniopteris hymenophylloides* (Brongn.): Sze, p. 184, pl. 1, figs. 2, 3. (Good sterile leaf. Jurassic; Inner Mongolia.)
- 1955 *Coniopteris hymenophylloides* (Brongn.): Lee, p. 44, pl. 2, figs. 1-3. (Sterile fragments. Shansi, China.)
- 1957 *Coniopteris hymenophylloides* (Brongn.): Stanislavski, p. 25, pl. 2, figs. 2-5. (Sterile and fertile pinnae. S. Russia.)

The following are considered distinct:

- 1905 *Coniopteris hymenophylloides* (Brongn.)?: Ward, p. 59, pl. 3, figs. 1-3. (Sterile and fertile fragments, fertile certainly not *C. hymenophylloides*. U.S.A.)
- 1925 *Coniopteris hymenophylloides* (Brongn.): Kawasaki, p. 7, pl. 6, fig. 23; pl. 13, fig. 44. (Two species, both with different venation. Korea.)
- 1938 *Coniopteris hymenophylloides* (Brongn.): Prinada, p. 372, pl. 5, fig. 2. (Perhaps = *C. furssenkoi* Prinada. Emba Region, Russia.)

EMENDED DIAGNOSIS. Leaf usually entirely sterile or almost entirely fertile. Sterile leaf as a whole linear lanceolate, width typically 8-12 cm. Rachis smooth, grooved above, rounded below; pinnae typically arising at an angle of about 80°, readily breaking off from the rachis, adjacent pinnae separated by gaps or only just meeting. Pinna in middle region of leaf linear lanceolate, scarcely tapering in proximal half but tapering steadily in distal half; pinnae from upper (and probably lower) parts of leaf tapering from base to apex. Lowest pinnules opposite,

borne at the very base, others becoming katadromically alternate. Basal pinnule with its first basiscopic lobe developed as filiform processes lying over the rachis, corresponding lobe of opposite pinnule also lying over the rachis but seldom filiform. Filiform processes best developed in lower and middle parts of leaf, becoming small towards the apex. Other pinnules on the two sides of a pinna usually equal, arising at an angle of about 70° , usually overlapping somewhat. Lamina divided into about 7 main lobes in larger pinnules divisions extending about two thirds the distance to the midrib. Lobes opposite, lowest basiscopic lobe smaller than the one opposite. Lateral veins usually arising opposite throughout the length of the pinnule. Largest lobes with a midrib and several laterals alternating katadromically. In lower pinnules (apart from the basal one) lobes more or less subdivided but apices usually rather obtuse; towards the pinna apex segments narrower, with a single vein and acute or almost linear. Midrib entering near the lower margin of the pinnule, upper margin deeply indented almost to the midrib, pinnule joined by a narrow wing of lamina extending along the rachis to the next pinnule. Lamina flat, without hairs, substance moderately thick.

Fertile leaf linear lanceolate, about as wide as sterile. Pinnae arising as in sterile leaf and bearing pinnules in the same order, but fertile pinnules reduced to a midrib bearing sori in pairs on the ends of short lateral lobes; in distal part of pinna sori borne singly on alternate reduced pinnules. Basal pinnules often partly sterile and with filiform processes extending over the rachis as in sterile leaf; upper pinnules usually wholly fertile apart from tissue at the sides of the midrib and occasionally a minute sterile lobe below the basal sorus, and occasionally also at the apex. Basal lobe often bearing two sori; others each bearing a single sorus on a stalk. Midrib region showing a central vein accompanied by some lamina, total width typically about 1 mm.; sorus stalks only slightly narrower, up to 1 mm. long, arising at about 45° to the midrib. In distal part of pinna, sorus borne on acroscopic side of a stalk about 1 mm. long and occasionally subtended by a minute sterile lobe below it, sterile lobe never filiform, nor extending far beyond the sorus.

Sorus with a cup-shaped indusium rather wider than the sorus stalk, smooth, membranous; placenta flat. Sporangia about 400μ long, 250μ wide, normally falling off after dehiscence.

Spores rounded-triangular with moderately thick very slightly mottled (almost smooth) walls. Mean width 40μ ($\sigma 5\mu$), range noted in one sporangium 32μ – 55μ . Triradiate cracks with a slight, ill-defined border. Sides of spores most often slightly concave, occasionally flat or slightly convex. (Abortive spores not seen.)

Lamina structure. The tissue of the lamina is not as delicate as the name *hymenophylloides* might suggest but just as thick as in such ferns as *Cladophlebis denticulata*. It is usually opaque, or a very dark brown, transmitting scarcely any light. Certain specimens have suffered natural maceration in being preserved and these are paler and show structure to transmitted light. The best of these are from Gristhorpe. The following cells are visible between the veins.

(1) elongated cells, elongated parallel with veins, about 20μ wide and 70μ long; perhaps upper epidermis;

(2) closely and evenly packed round cells 14μ wide, probably the palisade mesophyll;

(3) scattered oval cells $150\mu \times 50\mu$ (elongated in the direction of the veins). These are only conspicuous in a few specimens and even these are only locally preserved. They may be tannin sacs in the mesophyll.

The lower epidermis and stomata have not been recognised, but there is a very narrow

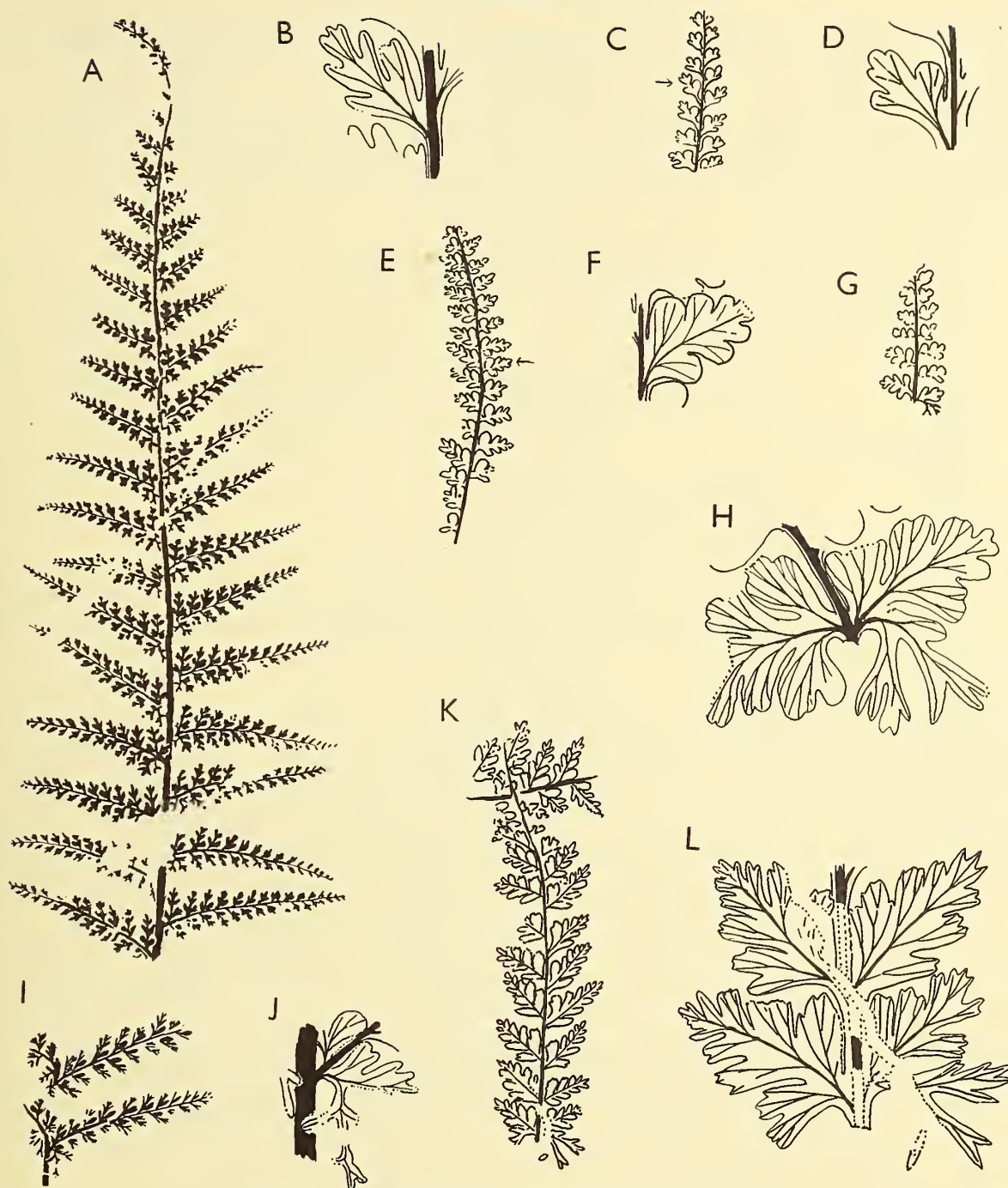


Fig. 53. *Coniopteris hymenophylloides* (Brongniart), sterile

A, upper part of finely divided leaf. Leckenby Coll., Sedgwick Museum, Cambridge, No. 357, $\times 1$. B, pinnule from A, $\times 4$. C, upper part of pinna, V.32008, $\times 1$. D, details of pinnule of C marked by arrow, $\times 4$. E, middle region of pinna, V.32009, $\times 1$. F, details of a pinnule of E, $\times 4$. G, unusual form of pinna (perhaps basal), V.32011, $\times 1$. H, base of a large pinna, V.32010, $\times 4$. I, finely divided form (half omitted) in which the basal pinnules overlap the rachis, V.32012, $\times 1$. J, details from I, $\times 4$. K, rather large pinna. Leckenby Coll., Sedgwick Museum, Cambridge, No. 373, $\times 1$. L, details of base of K, $\times 4$.

A, B, unlocalised. C–F, H, Gristhorpe Bed. G, Hawsker Maw Wyke. I, J, near Whitby. K, L, probably from Gristhorpe Bed.

band of fibres along the margins of the segments. At the apices of the lobes a single layer of large epidermal cells is seen and the vein ends in a slight enlargement close to them. It may be a hydathode.

DISTRIBUTION. *C. hymenophylloides* is abundant and widespread in the Lower and Middle Deltaic. The fertile leaf which is relatively rare is associated with the sterile leaf in the following localities:

Upper Deltaic:

Burniston Wyke (rare and fragmentary).

Middle Deltaic Gristhorpe Series:

Gristhorpe Bed.

Cloughton *A. nilssoni* Bed (no other fern present).

Fryup Head Coalpits.

Lower Deltaic:

Howdale, Robin Hood's Bay.

Beast Cliff *Equisetum* Bed.

Haiburn, *Zamites* Bed (with other species also).

In addition there is sterile material alone from seven other Lower Deltaic localities. I did not collect such material fully because I was unaware of the difficulty of discriminating between *Coniopteris* species, but had I done so it is likely that there would have been 50–100 Lower and Middle Deltaic localities.

DISCUSSION. *Coniopteris hymenophylloides* is based on Yorkshire material. Its scope as treated by Seward was somewhat too wide for it included certain Yorkshire specimens of *C. bella* and fertile fragments of *C. simplex*. As limited here *C. hymenophylloides* is still an abundant Yorkshire fossil but not nearly as well represented in old collections as had been thought; the rachis usually sheds its pinnae and so many of the large specimens are of *C. bella* or *C. murrayana*. It is of fairly constant form, the only proved variation is in the coarseness of division of the lamina, the variation being between the extremes of Text-fig. 53 A and 53 K. The more divided forms are *perhaps* what Phillips called *C. quinqueloba* but the agreement with his figure is imperfect. The extremes intergrade fully and share other diagnostic characters and no basis for dividing the series could be found.

The basal 'aphlebiform' lobes are constantly present though sometimes hidden by the rachis. They become small near the leaf apex. Other constant features are the small size of the basal acroscopic lobes of pinnules and the tendency of lobes to be opposite. The fertile leaf appears to be nearly constant; the fertile pinnae being reduced but having a certain amount of lamina along the midrib. Basal aphlebiform processes occur here also.

The fertile pinna had been excellently figured by Bunbury but unfortunately the rather different fertile fragments of *C. simplex* have been attributed to it. There is confusion also, at least in Museum collections, between *C. hymenophylloides* and *C. murrayana*.

COMPARISON. See p. 146 for *C. burejensis*, p. 158 for *C. murrayana*, p. 149 for *C. bella* and p. 142 for *C. simplex*.

The numerous foreign specimens attributed to *C. hymenophylloides* are hard to assess. Very few show the basal aphlebiform processes which seem constant in the Yorkshire material, but this may be merely because they are hidden.



Fig. 54. *Coniopteris hymenophylloides* (Brongniart), fertile

A-C, spores from the specimen shown in K, $\times 800$. D, base of fertile pinna. Manchester Museum, $\times 1$. E, details of an upper pinna of D, $\times 4$. F, transfer preparation of sorus from same block as D, $\times 20$. G, fragment showing a few sterile lobes, V.32086, $\times 4$. H, fertile pinna, V.31988, $\times 1$. I, isolated sporangium associated with a fertile pinna, in transfer, V.32087, $\times 40$. J, base of partly fertile pinna from same block as H, V.32013, $\times 1$. K, upper part of leaf. Manchester Museum No. LL.1448, $\times 1$. L, details of pinna from K, $\times 4$. In all the drawings $\times 1$, sori are shown in black whether the carbon substance remains or not.

A-C, K, L, labelled 'Haiburn Wyke J.W.J. April 1911'. D-F, I, Gristhorpe Bed. G, Beast Cliff *Equisetum* Bed. H, J, Cloughton *Anomozamites nilssoni* Bed.

The remarkable series of specimens figured by Brick (1937) show them well, but here there is a difference from the Yorkshire material in that the venation is different. In Brick's figures it is seen to be highly irregular in a way not yet seen approached in the hundreds of Yorkshire pinnules I have studied. Can this be an example of lateral displacement of veins in the mesophyll during compression, or alternatively, that the specimens are pathological? Some of Brick's larger specimens, notably pl. 4, fig. 1; pl. 5, fig. 1; pl. 9, fig. 2, appear to approach *C. burejensis*.

The specimens named *Davallia alfeizeranensis* Teixeira (1945) and *D. delgadoi* (Sap.) Teixeira (1948: 27, pl. 12, figs. 1-11, pl. 13, fig. 1-6) from the Lower Cretaceous look just like many Middle and Upper Jurassic ones determined by others as *Coniopteris hymenophylloides* (a few may be nearer *C. burejensis*). It would be interesting to know whether agreement extends to sporangia and spores. (The spores of the *Davallia* are very different from those of *Coniopteris*.)

Coniopteris murrayana (Brongn.) Brongniart

Text-figs. 55-57

1. Yorkshire specimens.

- 1834 *Pecopteris murrayana* Brongniart, p. 358, pl. 126, figs. 1-4 only. (Sterile specimens. Not fertile specimens (fig. 5) ? = *Aspidistes thomasi*.)
- 1849 *Coniopteris murrayana* (Brongn.) Brongniart, p. 105. (New genus for *P. murrayana* and for *Tympanophora racemosa*.)
- 1875 *Sphenopteris murrayana* (Brongn.) Phillips, p. 212 (in part). (Not lign. 26 copied from Brongniart, 1834, pl. 126, fig. 5.)
- 1875 *Sphenopteris arbuscula* Phillips, p. 216, lign. 36. (Sterile leaf.)
- ?1875 *Sphenopteris arbuscula* var., Phillips, p. 217, lign. 37.
- 1877 *Sphenopteris quinqueloba* var. *arbuscula* Lebour, p. 77, pl. 38.
- 1900 *Sphenopteris murrayana* (Brongn.): Seward, p. 155, pl. 21, fig. 5. (See below.)

2. Specimens from other regions.

- 1937 *Coniopteris*(?) *lobata* (Oldham & Morris): Brick, p. 31, pl. 9, fig. 1; text-fig. 12. (Good specimen. Central Asia.)
- 1937 *Coniopteris*(?) *kirgisica* Brick, p. 29, pl. 7, fig. 1; text-fig. 11. (Good sterile leaf. Central Asia.)
- ?1938 *Coniopteris furssenkoi* Prinada, p. 370, pl. 2, figs. 1-9; pl. 3, fig. 2. (Fragments, sterile similar, fertile different. Russia.)
- ?1957 *Hymenophyllites* cf. *zeilleri* Racib.: Stanislavski, p. 23, pl. 2, fig. 1; text-fig. 2. (Fertile fragments. S. Russia.)

3. The following are distinct:

- 1834 *Pecopteris murrayana* Brongniart, p. 358 (in part), pl. 126, fig. 5 only. (Fertile fragment discussed on p. 163. Figure repeated by Phillips, 1875.)
- 1864 *Tympanophora simplex* et *racemosa* Leckenby, p. 79. (Identified with *Sphenopteris murrayana* and here regarded as *Coniopteris bella* (p. 149).)
- 1876 *Thyrsopteris murrayana* (Brongn.) Heer, p. 30, pl. 1, fig. 4; pl. 2, figs. 1-4; pl. 8, fig. 11b. (Pinnules of different shape. Amurland.)
- 1894 *Thyrsopteris murrayana* (Brongn.): Raciborski, p. 180, pl. 10, figs. 15, 16; pl. 12, figs. 17-21. (Sterile and fertile. Poland.)
- 1905 *Thyrsopteris murrayana* (Brongn.): Ward, p. 61, pl. 8, fig. 4. (Sterile fern with acute pinnules. Jurassic; Oregon, U.S.A.)

EMENDED DIAGNOSIS. Sterile and fertile leaves similar and intergrading. Leaf large, 4-5 times pinnate; lamina as a whole broadly triangular; length exceeding 35 cm.; width exceeding 40 cm.; margins approaching rachis at leaf apex at an angle of 30°-40°. (Petiole unknown.) Main rachis up to 2.5 mm. broad, obscurely grooved above, bearing stiff hairs on



Fig. 55. *Coniopteris murrayana* (Brongniart)

A, details from main rachis of B, $\times 2$. B, outline (diagrammatically simplified) of V.3679, $\times \frac{1}{4}$. C, specimen V.3287, $\times 1$. A few cm. are omitted from the right and the top.

Both are from Yorkshire: exact locality unknown.

raised bases. Hairs multicellular, tapering to a point. Pinnae arising at an angle of about 70° , lowest at least 4 cm. apart but distance gradually diminishing upwards.

Primary pinna as a whole narrowly triangular, midrib situated near the basiscopic corner (the lowest basiscopic branches being short); branches of one pinna usually overlapping the next considerably. First pinnule on acroscopic side expanded into aphlebiform processes crossing the rachis, first pinnule on basiscopic side only slightly expanded.

Secondary pinnae arising in katadromic order and at an angle of 60° – 70° ; shape narrow triangular with the midrib situated near the basiscopic corner. Length up to 4 cm., width up to 1.5 cm., usually overlapping the next secondary pinna. Basal pinnules not expanded into aphlebiform branches. Tertiary pinnae arising in katadromic order and at an angle of 50° , midrib slender, almost smooth, composed of a central rib, accompanied by a wing of lamina, branches on the two sides equal except at the base where the lowest basiscopic pinnule is smaller than the one opposite. Quarternary branches (ultimate pinnules) arising in katadromic order or opposite, lower ones about twice as long as broad, margins obtusely lobed; venation a central midrib and lateral veins arising opposite or alternating katadromically.

Ultimate lobes varying in size in different leaves; largest about 1 mm. across; smallest about 0.5 mm. across. Basal lobes or branches of tertiary and higher orders never expanded in an aphlebiform manner. Secondary pinna rachis and smaller rachises smooth. Substance of lamina rather thick and often concealing the veins, margins often slightly incurved. Epidermal cells elongated along the veins, diverging at the sides. Lamina without hairs.

Fertile leaf (only known in fragments) branched as in sterile leaf, with some or all lobes of lamina slightly reduced and bearing a terminal sorus. Sorus small (about 0.5 mm. wide) usually pointing slightly downwards. Indusium forming a strongly flattened cup, margins slightly lobed, tissue of indusium fairly thick, except near the edge.

Sporangia rather small, 200μ wide, only 1–3 emerging at a time; annulus well developed. Spores rounded-tetrahedral, mean diameter 45μ σ 5μ ; walls of medium thickness, slightly mottled or almost perfectly smooth. Margins of triradiate crack only slightly thickened, margo undeveloped.

Variation. The material is inadequate to show variation in the shape of the whole leaf but there is obvious variation in the size and shape of the ultimate pinnules. The commonest form lies between the limits shown in Text-fig. 55 A–C, and the leaf in Text-fig. 56 D. Specimens as coarse as in Text-fig. 56 G or as fine as Text-fig. 56 C and 56 H are unusual. It is also possible that the very coarse form (Text-fig. 56 G) may represent a distinct species. Such specimens occur chiefly in the Middle Deltaic while the medium and finer ones occur in the Lower Deltaic. The specimen figured by Seward (1900b, pl. 21, fig. 5) is from the Middle Deltaic and coarsely divided. All the fertile fragments I have collected are from the Lower Deltaic and associated with finely divided sterile leaves. The fertile fragments were identified by their intergradation with sterile forms and by their association with them, sometimes in the absence of any other fern.

Mesophyll structure. The lamina is too thick to transmit light as ordinarily preserved but transfers show slightly elongated epidermal cells. A very few specimens which have suffered natural maceration are translucent and look much like similar specimens of *C. hymenophylloides*. Longitudinal rows of round bodies 25μ wide (? palisade cells) are conspicuous. One fragment shows rather large oval secretory cells, $250\mu \times 150\mu$, arranged in single file each side of the

veins (not scattered in the mesophyll). They are only obscurely seen in other associated fragments. In some fragments the veins are slightly expanded just below the apices (? hydathodes).

DISTRIBUTION. Sterile leaves of *C. murrayana* are widespread in the Lower and Middle Deltaic. The list of localities below is probably incomplete as the species was not distinguished in my earlier collecting. Fertile fragments are known from four localities only but as the small sori are inconspicuous they may be common.

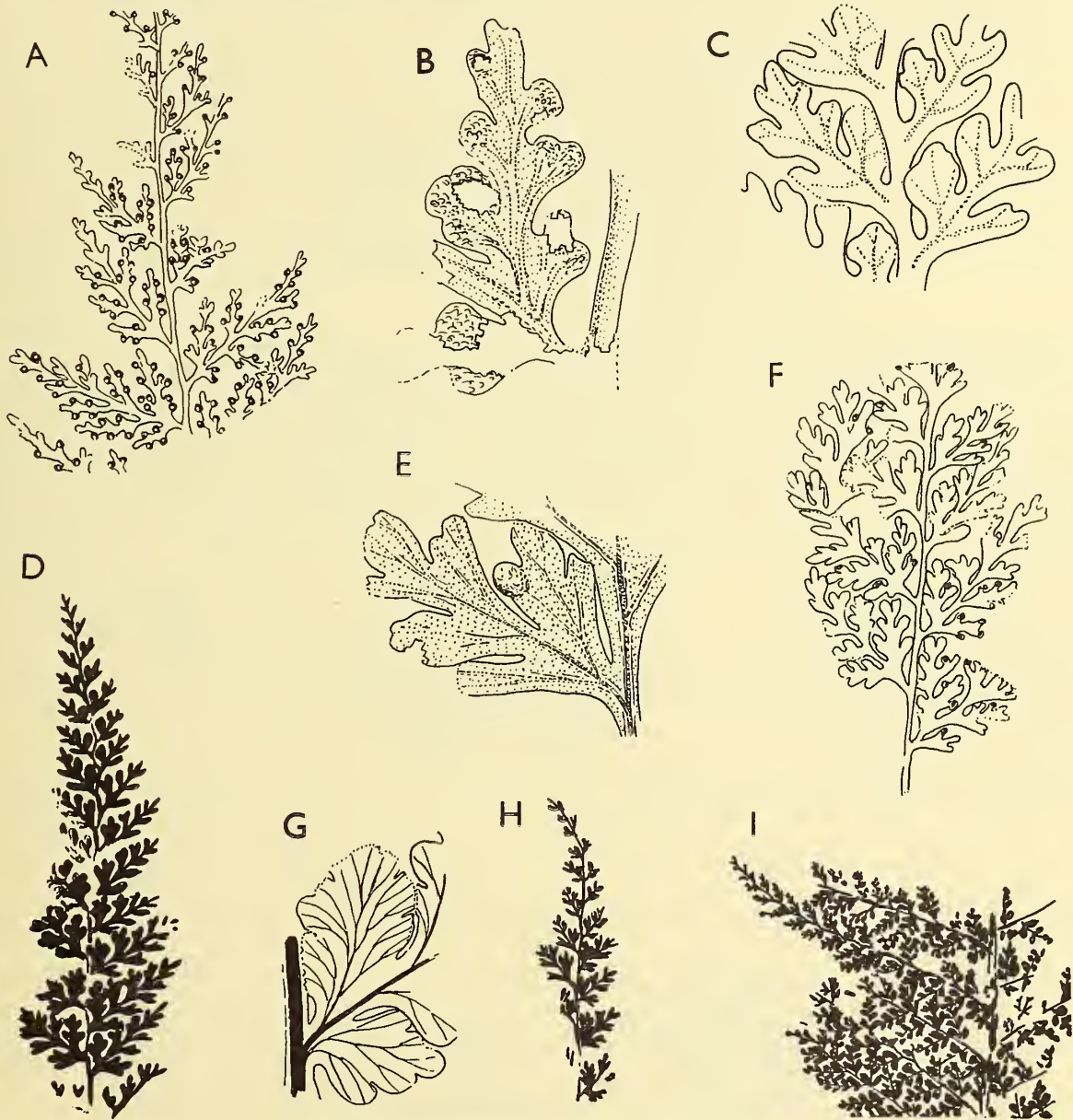


Fig. 56. *Coniopteris murrayana* (Brongniart)

A, fertile secondary pinna, V.32063, $\times 2$. B, details from A, $\times 8$. C, details from H, $\times 8$. D, sterile secondary pinna, V.32065, $\times 2$. E, details from the small fragment in F, $\times 8$. F, partly fertile fragments, V.32066, $\times 2$. G, sterile pinnules (coarsely lobed form), V.32071, $\times 4$. H, sterile secondary pinna (see also C), exceptionally finely lobed form, V.32064, $\times 2$. I, part of a large primary pinna (most of specimen omitted). Yorkshire Museum, $\times 1$.

All specimens from Haiburn Wyke.

The following records are of sterile material only unless otherwise mentioned:

Middle Deltaic, Gristhorpe Series:

Gristhorpe Bed (Lebour's 1877 specimen; also specimen in Manchester Museum.

Cloughton Wyke, *Solenites* Bed.

Cloughton Wyke, *qunqueloba* Bed.

Lower Deltaic:

Hasty Bank.

Eskdaleside 'New' alum pit.

High Whitby, below fog signal, sterile and fertile.

Hawsker, Maw Wyke, sterile and fertile.

Whitby, fallen blocks in Rail Hole Bight.

Beast Cliff, *Elatides* Bed, sterile and fertile.

Haiburn Wyke, *Zamites* Bed, sterile and fertile. Probable origin of Phillips' specimen.

The large specimens in the old collections are imperfectly localised.

DISCUSSION. It is surprising that *C. murrayana*, the type species of *Coniopteris*, has faded into oblivion as there are the two fine slabs in the British Museum (V.3287 and V.3679) and almost equally good ones in the Leckenby Collection at Cambridge; fragments are moderately common. The species almost ceased to be recognised after Seward discussed it in 1900. The

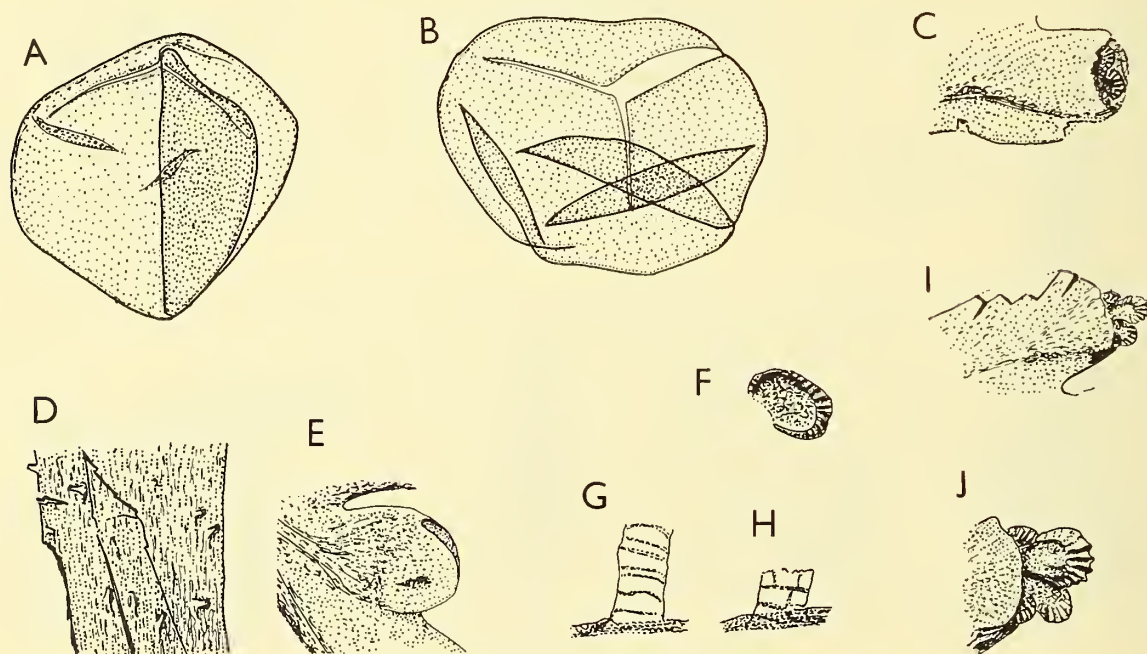


Fig. 57. *Coniopteris murrayana* (Brongniart)

A, B, spores, V.32066a, $\times 800$. C, sorus in transfer, V.32067, $\times 20$. D, rachis showing hair bases, in transfer, V.32074, $\times 20$. E, empty sorus in transfer, V.32067, $\times 20$. F, associated sporangium fragment, V.32067, $\times 40$. G, H, hairs on rachis in transfer, V.32074, $\times 100$. I, sorus in transfer, V.32067, $\times 20$. J, details from I, $\times 40$.

All specimens from Haiburn Wyke.

reason may be that Seward expressed the view that it was doubtfully distinct. 'It is hopeless to attempt a complete synonymy of *Sphenopteris Murrayana* as employed in the present sense, as the greater number of fossils so named by various authors should be referred rather to *C. hymenophylloides*'. He mentioned the two large specimens (Text-fig. 55) but only figured an isolated fragment. This fragment is preserved on a slab (39273) of the characteristic Gristhorpe matrix and shows five other similar sterile fragments. It is associated also with two fertile pinnules resembling *C. bella* or *C. hymenophylloides* but not *C. murrayana*. The sterile pinnules are more coarsely divided than normal *C. murrayana*, and the fertile pinnules are certainly distinct. I prefer not to identify the specimens on this slab.

Brongniart founded his genus *Coniopteris* with *C. murrayana* as its type species. *Tympanophora racemosa* was to be its fertile form, but it probably belongs to another species. Earlier he had attributed a quite different fertile specimen (1834, pl. 126, fig. 5) to *C. murrayana* but evidently had changed his view by 1849. He was right in rejecting pl. 126, fig. 5, the pinnae are long lanceolate and the first basiscopic pinnule is not reduced in size. It looks like a fertile leaf of *Aspidistes thomasi*.

The two species *Coniopteris lobata* and *C. (?) kirgisica* described and figured by Brick (1937) are considered identical with the specimens described here.

CLASSIFICATION AND COMPARISON. Brongniart's figures show good fragments with triangular primary or secondary pinnae and more or less ovate ultimate lobes. The basal pinnules are conspicuously unequal but no aphlebiae are seen on the rachis (if indeed the main rachis and not a large pinna is figured). The specimens figured here are identical with those in Brongniart's pl. 126, figs. 1-4, but as pointed out above, his fig. 5 is distinct. *C. hymenophylloides* is distinguished below:

<i>C. hymenophylloides</i>	<i>C. murrayana</i>
Width of a leaf typically 8-12 cm. Lamina long lanceolate. Rachis smooth. Primary pinnae scarcely tapering in lower half.	Width up to 40 cm. Lamina broadly triangular. Rachis bristly. Primary pinnae tapering from base.
First pinnule on basiscopic side aphlebiform. Pinnae and pinnules seldom overlapping.	First pinnules on acroscopic side aphlebiform. Pinnae and pinnules usually overlapping greatly.
Lower pinnules on two sides nearly equal.	Lower pinnules on basiscopic side reduced.
Pinnules (secondary branches) at first opposite, gradually becoming katadromic.	Secondary and tertiary branches katadromic from the first.
Fertile leaf much reduced.	Fertile leaf not much reduced.
Sorus about 1 mm. wide, stalked. Indusium not much flattened.	Sorus about 0.5 mm. wide, merged in lamina. Indusium strongly flattened.
Numerous sporangia ripening together and then falling off.	Only a few sporangia ripening at a time.

Confusion is also possible between small fragments of *C. simplex* and of the most finely divided forms of *C. murrayana*. In *C. murrayana*, however, some lobes with two or more veins are always to be found. For *Sphenopteris metzgerioides*, see p. 193.

Small fragments of *C. murrayana* cannot be satisfactorily distinguished from sterile *Stachypteris spicans*. As a rule *Stachypteris* leaves seem to be much more sparsely branched and

the rachis is not channelled; presumably, however, collapse can occur in compression. Its lamina is perhaps a little thicker. The mode of branching seems the same. As far as is known *Stachypteris* is never bristly but as the bristles only occur on the larger rachis branches of *C. murrayana* this may not help.

Pecopteris lobata Oldham & Morris (1863: 52) is rather like *C. murrayana* but is distinguishable by (1) the absence of aphlebiform processes crossing the main rachis, and (2) by the equal size of secondary branches on the upper and lower sides (indeed the lower ones seem slightly larger). In *C. murrayana* they are reduced to about half the size of the opposite ones near the base of a pinna. Halle (1913) has figured specimens from Antarctica as *Coniopteris*(?) *lobata* (Oldham).

Coniopteris margaretae sp. nov.

Text-fig. 58

DIAGNOSIS. (Shape of leaf as a whole unknown, but regarded as bipinnate for description.) Fertile leaf almost wholly fertile; rachis in middle region slender, about 2 mm. thick, bearing pinnae about 6 cm. long at intervals of about 7 mm. Main rachis and pinna rachis rounded below, grooved above; under surfaces bearing stiff outward pointing bristle bases, upper surface smooth. Bristles occurring at a concentration of about 10 per sq. mm., base solid about 40μ thick (free part usually broken off before preservation). First pinnule arising close to the rachis on the acroscopic side, later pinnules often opposite on the two sides. Pinnules of one pinna usually overlapping those of the next and the adjacent pinnules of the same pinna. Typical pinnule consisting of a very short stalk, forking after about 1 mm. into a forward pointing fertile branch and an outward pointing sterile branch; sterile branch often forked once more into two sterile lobes, 0.4 mm. broad. First pinnule varied, sometimes bearing two or three sori, sometimes with more than two sterile lobes, projecting more or less over main rachis. Substance of sterile lobes fairly thick, upper surface marked with uniform elongated cells, lower surface with elongated cells in the middle, shorter ones at the sides, vein not otherwise distinguished, small bristles only present and confined to base of the under side.

Stalk of sorus resembling sterile lobes. Sorus and indusium (in lateral compression) semicircular to half-moon shaped, inner end often overlapping pinna rachis. Total width of indusium 4–5 mm., height from top of stalk to free edge about 2 mm., thickness (side to side of indusium) 1.5–2 mm., basal sori sometimes smaller and hemispherical. Sorus lying in the horizontal plane, or tilted slightly downwards; indusium rather thick, marked externally with elongated cells 25μ wide, upper and lower sides exactly similar, margins entire. Placenta broad, flat, ultimately shedding all its sporangia but retaining some short filamentous hairs 20μ wide. Sporangia numerous, not projecting beyond the edge of the indusium; about 250μ wide, annulus well developed, probably complete, but very unequally thickened.

Spores very large, rounded—tetrahedral; mean diameter 74μ (smallest and largest noted, apart from a few very small ones presumed abortive, 65μ and 88μ); wall rather thick, smooth. Triradiate crack with a distinctly thickened margo; triradiate crest sometimes rather prominent and projecting as a delicate ridge 2μ high.

DISCUSSION. This rare fern is only known from one point in the Cloughton *quinqueloba* Bed (Middle Deltaic) where it was collected by my daughter after whom it is named. The holotype shows two similar fragments, lying the same way up and parallel; it is possible that

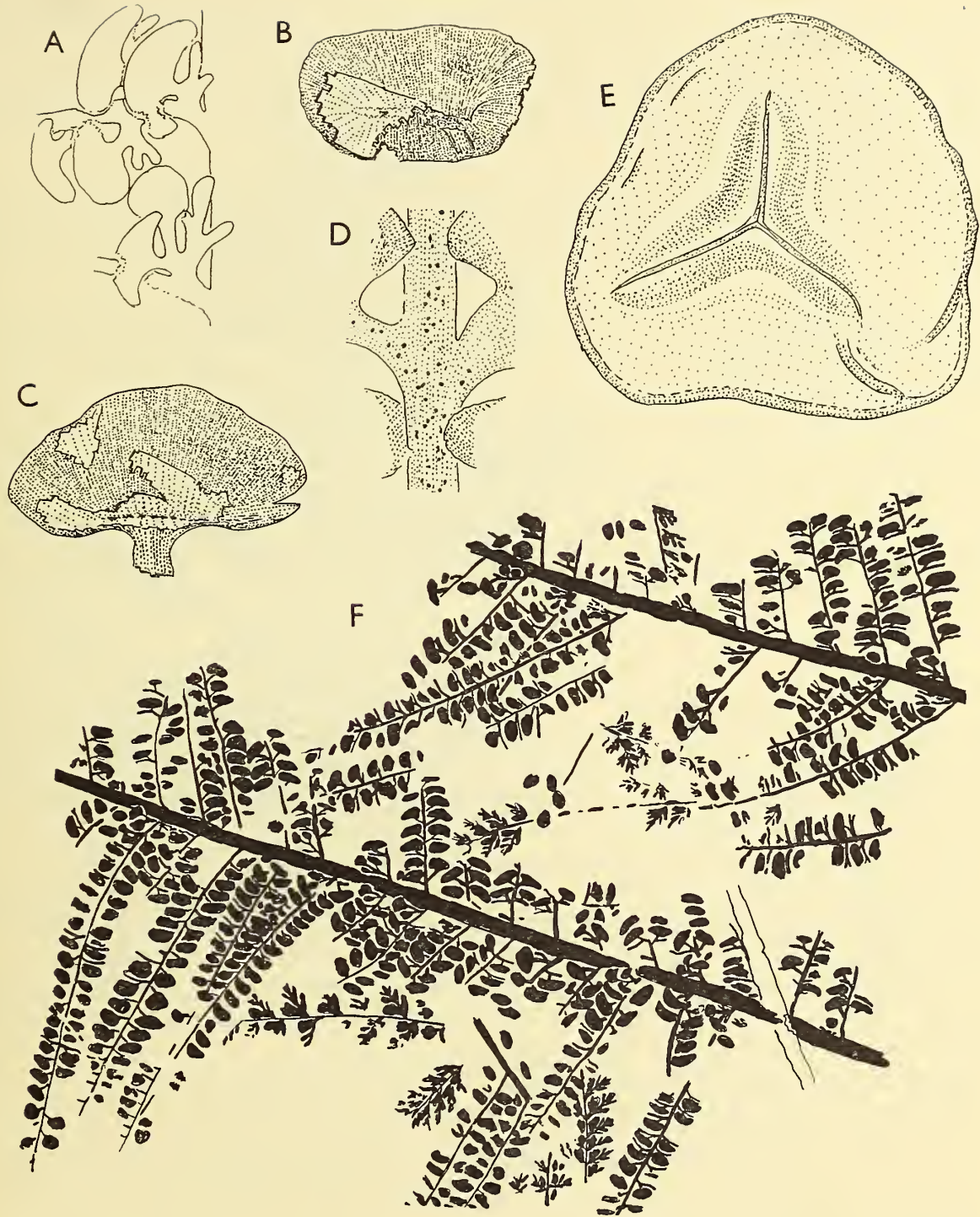


Fig. 58. *Coniopteris margaretae* sp. nov.

A, sori and sterile lobes; the main rachis is to the right, from near base of the lower leaf in F, $\times 4$. B, single sorus compressed nearly vertically, part of the indusium has been picked away to expose the placenta, V.32265, $\times 10$. C, adjacent sorus to B, compressed nearly laterally, placenta similarly exposed, $\times 10$. D, imprint of under side of a pinna rachis showing bristle bases, from the upper leaf in F, $\times 10$. E, vertically compressed spore, V.32264a (from F), $\times 800$. F, holotype (lower leaf), a few cm. at all sides are omitted. Associated sterile fragments are *C. hymenophylloides*, V.32264, $\times 1$.

All specimens are from Cloughton *quinkeloba* Bed.

they are really pinnae of a very large leaf and not each from a single leaf as assumed. A few smaller fragments are known, some, and perhaps all, are from the holotype.

No sterile leaf is known; a few sterile pinnae of *Coniopteris* occur with it, but these are ordinary *C. hymenophylloides*; they differ in their fine features of venation and particularly in having no bristles on their rachises.

The indusium is remarkably robust and its form is particularly clear in this species. Although most sori are compressed laterally, a number are compressed obliquely or vertically, and prove that the indusium is continuous, but its shape is elongated. It is more boat-shaped than cup-shaped (except that there is no keel). A few of the basal sori are, however, rounded cups.

The anadromic arrangement of the pinnules is exceptional in *Coniopteris*. It was hard to make out the true arrangement, because of the overlap of the sori, but by comparison of part and counterpart, it is evident that this arrangement is constant.

COMPARISON. *C. margaretæ* is rather like *C. simplex* but differs in its far larger sori, which are also more crowded. Its spores also are very much larger. It is less like the other species of *Coniopteris*, but it somewhat resembles *Gonatosorus sphenopteroides* Brick (1937: 34, pl. 10, figs. 1-3; text-fig. 15). *G. sphenopteroides*, however, has shorter sterile lobes and a much smaller sorus; the shape of its indusium is not clear. *G. nathorsti* Raciborski (1894) is less similar having broader and undivided sterile lobes, and also a smaller sorus.

Genus KYLIKIPTERIS nov.

DIAGNOSIS. Leaf large, repeatedly pinnate, branching katadromic throughout. In sterile parts, pinnules Pecopterid with forked and diverging lateral veins. In fertile parts pinnules reduced to a stalk bearing a robust hemispherical cup-shaped indusium. Placenta long and club-shaped, in middle of indusium. Sporangia numerous, rather small, falling after dehiscence. Spores smooth with a triradiate scar.

TYPE SPECIES. *Kylikipteris arguta* (Lindley & Hutton).

REMARKS. *K. arguta* is now removed from *Coniopteris*. Apparently Brongniart, to judge from Leckenby's remarks, recognised that it was worthy of generic rank, but it has either been included in *Coniopteris* or, where the sterile leaf alone was considered, in *Cladophlebis*.

K. arguta differs considerably in its long placenta both from the holotype of *Coniopteris murrayana* and from the more familiar *C. hymenophylloides*. It differs also in its Pecopterid sterile pinnules, all others being Sphenopterid.

The name is from *Κυλίξ* a stalked wine cup and refers to the shape of the sorus.

Kylikipteris arguta (Lindley & Hutton) n. comb.

Text-figs. 59-61

1. Yorkshire specimens.

- 1834 *Neuropteris arguta* Lindley & Hutton, p. 67, pl. 105. (Two sterile secondary pinnae, veins.)
- 1835 *Pecopteris acutifolia* Lindley & Hutton, p. 13, pl. 157. (Sterile secondary pinna.)
- 1838 *Pecopteris Lindleyana* Sternberg, p. 153. (Name.)
- 1864 *Pecopteris arguta* (L. & H.) Leckenby, p. 79, pl. 10, fig. 4. (Top of good partly fertile pinna. Original in Leckenby Coll.)
- 1875 *Pecopteris Lindleyana* Sternb.: Phillips, p. 209, lign. 22. (Partly fertile pinna, sorus, veins.)



Fig. 59. *Kylikopteris arguta* (L. & H.), sterile

A, regarded as the apex of a primary pinna. Leckenby Coll., No. 107, Sedgwick Museum, Cambridge, $\times 1$. B, details from A, $\times 2$. C, transfer preparation by transmitted light showing veins and some of the secretory cells (obscure ones omitted), V.27059, $\times 8$. D, typical sterile pinnules. Leckenby Coll., No. 114, Sedgwick Museum, Cambridge, $\times 2$. E, exceptionally large pinnule. Leckenby Coll., No. 104, Sedgwick Museum, Cambridge, $\times 4$.

All the figures are reproduced from Harris (1947, text-figs. 3 B, C; 5, 6 F, H).

- 1900 *Coniopteris arguta* (L. & H.) Seward, p. 115, pl. 16, fig. 3, 3a; pl. 17, figs. 4, 5; text-fig. 16. (Parts of sterile and fertile pinnae, veins, sorus.)
 1946 *Coniopteris arguta* (L. & H.): Harris, p. 363. (Comparison with *Klukia exilis*.)
 1947 *Coniopteris arguta* (L. & H.): Harris, p. 400, text-fig. 3 B-E, 4-6. (Sterile and fertile leaf, sorus.)
 1947 *Cladophlebis arguta* (L. & H.): Frenguelli, p. 15, text-fig. 1a. (Discussion of Yorkshire specimen, copy of Lindley & Hutton's figure. Fertile Yorkshire material rejected.)

2. Specimens from other regions.

The following sterile specimens are possibly identical, but none is sufficiently characterised.

- 1876a *Asplenium argutulum* Heer, p. 47, pl. 3, fig. 7; pl. 19, figs. 1-4. (Sterile. Amurland.)
 1883 *Asplenium argutulum* Heer: Schenk, p. 246, pl. 46, figs. 2-4; pl. 47, figs. 1, 2. (Sterile. China.)
 1911a *Coniopteris arguta* (L. & H.): Seward, p. 666, pl. 4, figs. 58, 59; pl. 8, fig. 34. (Sterile fragments. Upper Jurassic; Scotland.)
 1913 *Cladophlebis* (*Coniopteris*?) *arguta* (L. & H.): Halle, p. 15, pl. 2, figs. 1-3, 5. (Sterile. Graham Land. Referred to *C. grahami* by Frenguelli.)
 1922 *Cladophlebis arguta* (L. & H.): Johansson, p. 25, pl. 7, fig. 11. (Sterile. Lower Lias; Sweden.)
 1933 *Cladophlebis arguta* (L. & H.): Sze, p. 24, pl. 4, figs. 1-4. (Sterile leaves. China.)
 1933 cf. *Cladophlebis arguta* (L. & H.): Sze, p. 15, pl. 10, figs. 10, 11. (Sterile fragments. China.)
 1933c cf. *Cladophlebis arguta* (L. & H.): Sze, p. 81, pl. 12, figs. 1, 2. (Sterile. Shensi, China.)

DIAGNOSIS. Sterile and fertile parts occurring in same leaf. Leaf very large; possibly 50 cm. wide (length unknown). Petiole obscurely longitudinally striated, about 12 mm. thick. Main rachis stout, giving off pinnae laterally at an angle of about 70° near the apex (origin of lower pinnae unknown). Larger rachises not appearing channelled but smaller branch rachises channelled above. Larger rachises showing obscure longitudinal ridges, otherwise smooth, hairs andramenta absent. Smaller rachises smooth. Branching in katadromic order throughout the leaf; branches rather crowded and sterile pinnules often overlapping. Primary pinnae lanceolate, at least 17 cm. long (larger ones probably much longer); width of primary pinna up to 20 cm.; apex acute. Secondary pinnae arising at right angles below but at 60°-70° above, equal in length on the two sides. Tertiary branches (pinnules) typically oblong 6 mm. × 1.1-1.5 mm. (largest 10.0 × 2.9 mm.). In large pinnules, margins showing rounded lobes about 1.5 mm. wide; in medium-sized ones lobing weaker, in small pinnules margins entire. Base of pinnule typically neither expanded nor contracted but slightly contracted in the largest pinnules. Apex obtuse. Pinnules on the two sides equal except for a short first basiscopic one, often with a basal lobe projecting towards or onto the pinna rachis. Lamina flat or slightly convex but margins never reflexed; without hairs on either side. Midrib fairly conspicuous but slender; lateral veins inconspicuous, typically making an angle of 45°-60° to the midrib; lowest forked twice; upper ones forked once, concentration of veins at the margin about 25 per cm. Adjacent pinnules joined by a flange of lamina. Substance of lamina moderately thick, showing dark (? secretory) cells about 35μ wide scattered evenly or bordering the veins.

Fertile parts tending to occur below sterile parts (at leaf apex and on individual pinnae). In fully fertile parts, pinnule reduced to a tapering stalk 4 mm. long, bearing a single stalked apical sorus; sorus tilted downwards, in partly fertile parts lamina of pinnule more or less developed. Substance of indusium thick, smooth inside and outside. Sporangia falling at maturity. Placenta about 1 mm. long, central, covered with short sporangial stalks. Sporangia about 200μ in diameter, spores rounded; mean diameter about 44μ; walls moderately thick, almost smooth. Margo scarcely thickened.

DISTRIBUTION. *K. arguta* is uncommon. Sterile fragments have been found in the Lower Deltaic Beast Cliff *Ptilophyllum* Bed, also in the Middle Deltaic Cloughton *Solenites* Bed and

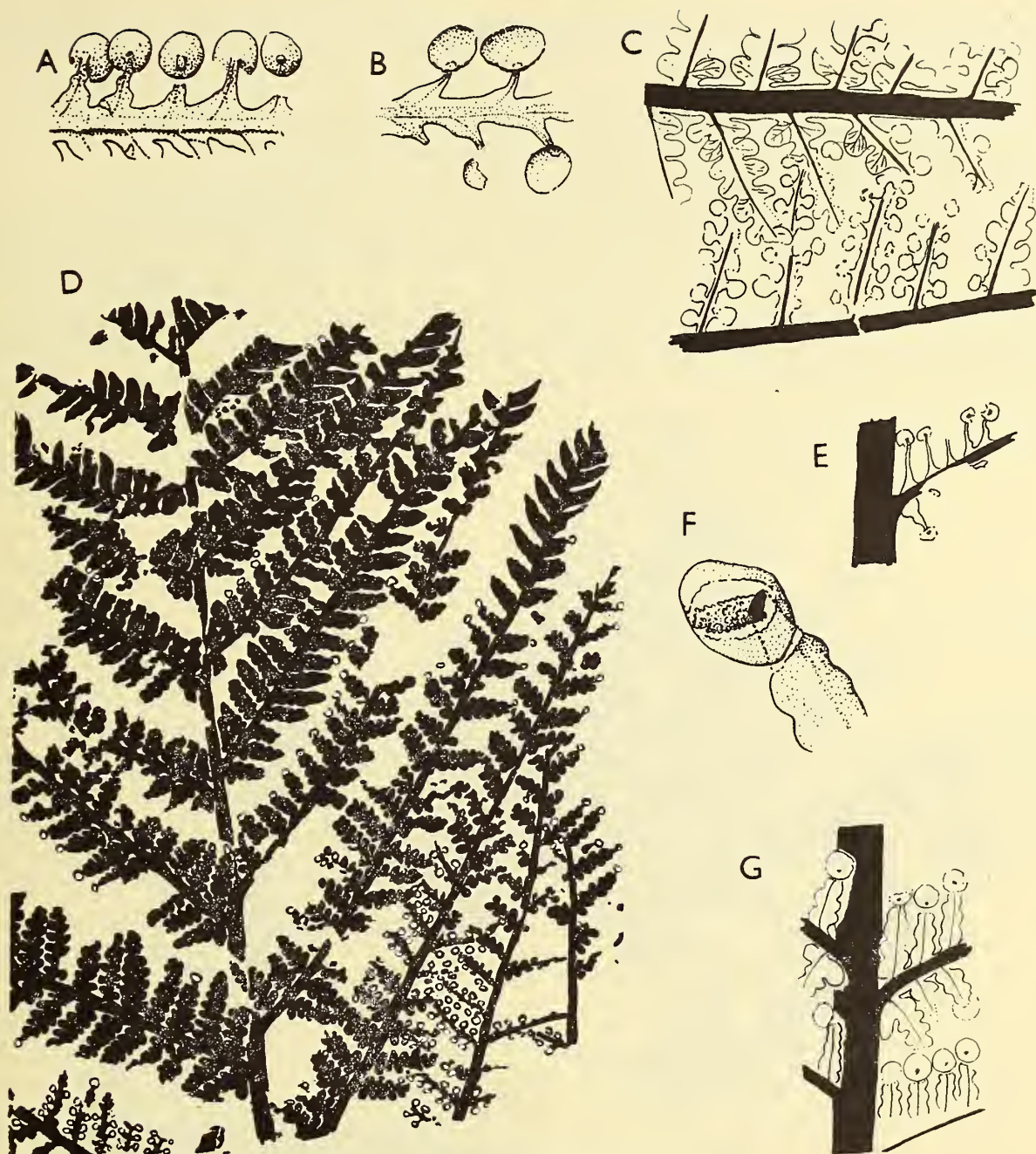


Fig. 60. *Kyliopteris arguta* (L. & H.), fertile

A, distal part of a fertile segment seen from above, $\times 4$. B, similar specimen seen from below, $\times 4$. Both specimens from Leckenby Coll., No. 112, Sedgwick Museum, Cambridge. C, details of lower pinnae of D, $\times 2$. D, regarded as a leaf apex. Leckenby Coll., No. 110, Sedgwick Museum, Cambridge, $\times 1$; 5 cm. are omitted on the left. E, fertile pinnules with little lamina. Leckenby Coll., 114, Sedgwick Museum, Cambridge, $\times 2$. F, sorus dissected to expose the placenta. The base of the placenta is shown in black and the top of the pinnule which was removed is shown by a broken line. Leckenby Coll., Sedgwick Museum, Cambridge, $\times 15$. G, fertile pinnules with a well-developed lamina. Leckenby Coll., 112, Sedgwick Museum, Cambridge, $\times 2$. All the figures are from Harris (1947, text-figs. 3 D, E; 4; 6 A, B, E, G).

All specimens are probably from Cloughton Wyke *Solenites* Bed.

the Gristhorpe Bed. The Museum fertile specimens appear to be from both of these Middle Deltaic localities. Fertile fragments also occur in the tips of old coal pits at Bransdale, Ouse Gill (Middle Deltaic).

DISCUSSION. Many good specimens of *K. arguta* exist in the Leckenby Collection at Cambridge and some elsewhere but I have only found fragments.

The leaf is certainly very large and is only known from fragments; two leaf apices are figured here and a number of primary pinnae. The leaf apex is distinguishable from the pinna by its more obtuse shape and the very rapid change in passing up it; other distinguishing features are given by Harris (1947). The lower part of the main rachis is unknown but there are some petiole fragments associated with the lamina fragments which are attributed to it. Several of the larger leaf fragments are sterile above but become fertile below or if somewhat

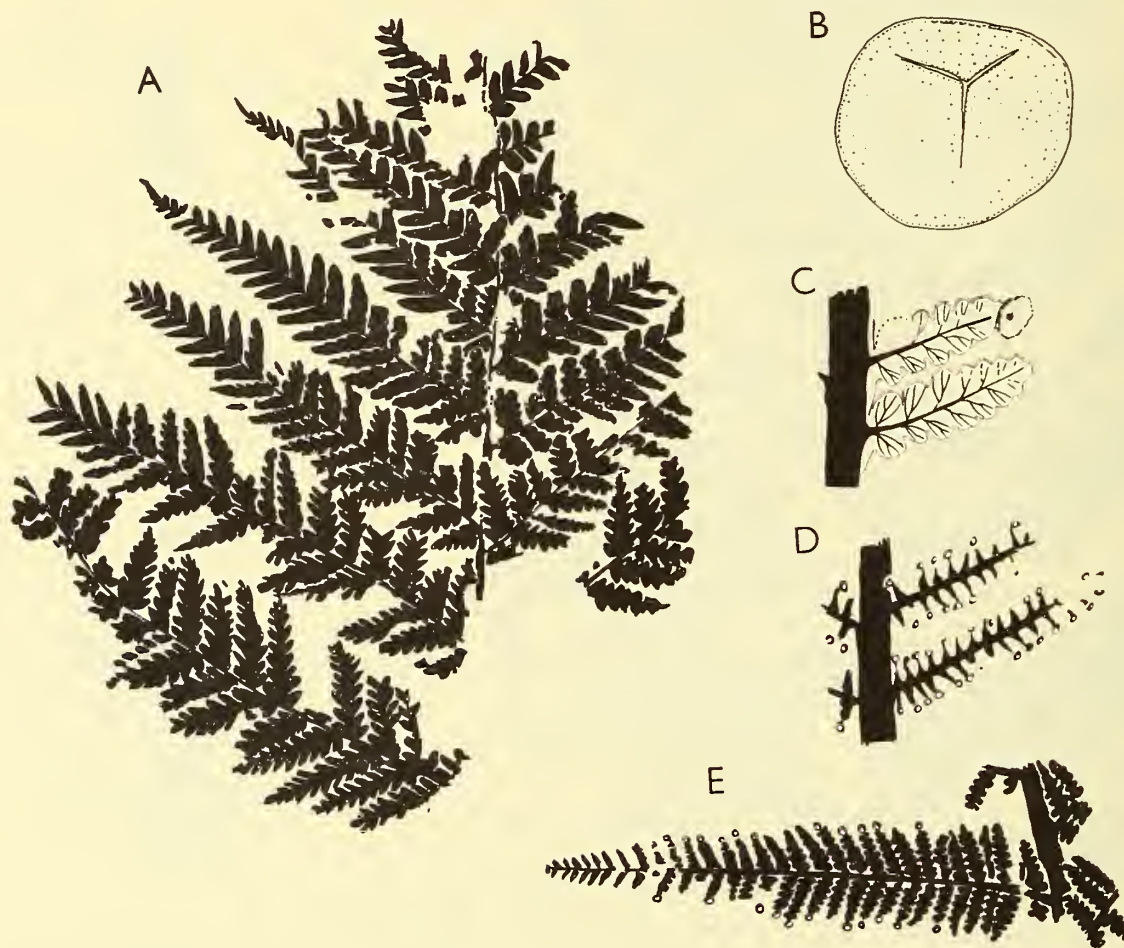


Fig. 61. *Kyliopteris arguta* (L. & H.)

A, sterile leaf apex. Leckenby Coll., K.113, Sedgwick Museum, Cambridge, $\times 1$. (A few cms. on the right are omitted). B, spore from Leckenby Coll., K.110, Sedgwick Museum, Cambridge, $\times 800$. C, two pinnules from E, $\times 4$. D, about half of a fragment of a large fertile pinna. Leckenby Coll., K.102, Sedgwick Museum, Cambridge, $\times 1$. E, lower secondary pinna from a large pinna, the upper 15 cm. being sterile. Leckenby Coll., K.111, Sedgwick Museum, Cambridge, $\times 1$. All specimens unlocalised. The matrix of A and D suggests the Gristhorpe Bed, that of E the Cloughton Wyke *Solenites* Bed.

fertile above they are more fertile below with suppression of the lamina. This is seen, for example, in the specimen figured by Leckenby (1864) where all the lower part (omitted from the figure) is fully fertile.

A balsam transfer of a fertile fragment fully confirmed the figure of the placenta given here, but it showed nothing new. All the sporangia had fallen, as in nearly all specimens studied. One sorus, however, apparently retaining all its sporangia was found in the Leckenby Coll. no. 110. One sporangium was macerated. Its spores did not separate well enough for a count, but the number is not large. Their walls are moderately thick and nearly smooth and the shape is rounded.

COMPARISON. The fertile pinna of *K. arguta* is unique. The only Yorkshire ferns resembling sterile *K. arguta* are *Klukia exilis* (see p. 128) and *Aspidistes thomasi* (p. 182). Fertile *K. arguta* is not known outside Yorkshire but a number of rather similar sterile fragments are known in various floras. Some of the specimens of sterile *Cladophlebis* leaves described as *C. arguta*, *C. whitbiensis*, *C. dunkeri* and *C. browniana* are somewhat like the less well characterised fragments of *K. arguta*.

Genus EBORACIA Thomas, 1911a:387

DIAGNOSIS. Leaf bipinnate, pinnules of Pecopterid form and venation. Sori marginal with an elongated placenta surrounded by a cylindrical indusium. Sporangia shortly stalked with a well-developed annulus. Spores smooth, rounded-tetrahedral.

This diagnosis is taken with slight modification from Wilson & Yates (1953), the first to give differentiating characters. *Eboracia* has the continuous indusium of the Thyrsopterideae and differs from *Coniopteris* as ordinarily used (e.g. *C. hymenophylloides*) in its longer placenta and cylindrical indusium, from *Kylikopteris* (*Coniopteris*) *arguta* in its cylindrical indusium and lateral rather than terminal sorus, and from *Coniopteris murrayana* in its long placenta, cylindrical indusium and much more numerous sporangia.

Eboracia lobifolia (Phillips) Thomas

Text-figs. 62, 63

1. Yorkshire specimens.

- 1829 *Neuropteris lobifolia* Phillips, p. 148, pl. 8, fig. 13. (Holotype, sterile.)
- 1833 *Neuropteris undulata* Lindley & Hutton, p. 7, pl. 83. (Sterile; drawing incorrect but emended, 1837.)
- 1835 *Neuropteris lobifolia* Phillips: Phillips, p. 119, pl. 8, fig. 13. (As 1829.)
- 1837 *Pecopteris lobifolia* (Phillips) Lindley & Hutton, p. 79, pl. 179. (Good sterile leaf.)
- 1875 *Pecopteris lobifolia* (Phillips): Phillips, p. 210, pl. 8, fig. 13. (Brief description. Figure as 1829.)
- 1875 *Pecopteris undulata* (L. & H.) Phillips, p. 211. (Brief description.)
- 1900 *Cladophlebis lobifolia* (Phillips) Seward, p. 145 (in part), pl. 15, fig. 6 (good sterile leaf); text-figs. 22, 23 (fertile pinnae). Not text-figs. 20, 21 (perhaps *Todites williamsoni*).
- 1911a *Eboracia lobifolia* (Phillips) Thomas, p. 387, text-fig. (New genus, spores figured.)
- 1911 *Eboracia lobifolia* (Phillips): Seward, pp. 13, 41, pl. 7, fig. 73. (Sterile leaf, Leckenby Coll., K.81.)
- 1953 *Eboracia lobifolia* (Phillips): Wilson & Yates, p. 934, text-fig. 3. (Sterile and fertile, sorus, spores.)

2. Specimens from other regions.

- 1892 *Asplenium lobifolium* (Phillips) Bartholin, p. 19, pl. 8, figs. 1, 2. (Sterile leaves. Bornholm.)
- 1894 *Dicksonia lobifolia* (Phillips) Raciborski, p. 177, pl. 11, figs. 1-7; pl. 12, figs. 1-3, 5, 6; pl. 25, fig. 14. (Good sterile and fertile leaves. Poland.)

- 1894 *Dicksonia lobifolia crenifolia* Raciborski, p. 180, pl. 12, fig. 4. (Sterile. Poland.)
 1911 *Eboracia lobifolia* (Phillips): Seward, pp. 13, 41, pl. 2, figs. 20, 20 A-26 B. (Sterile and fertile, spores. Central Asia.)
 1911 *Cladophlebis lobifolia* (Phillips): Thomas, p. 64, pl. 2, fig. 14, 14a, 14b. (Sterile. Izium, Russia.)
 1933 *Cladophlebis* (*Eboracia* ?) *lobifolia* (Phillips): Yabe & Oishi, p. 208, pl. 30, figs. 9, 9a. (Sterile leaf. Manchuria.)
 1933c *Cladophlebis* (*Eboracia*) *lobifolia* (Phillips): Sze, p. 80, pl. 11, figs. 16, 17, 20-22; pl. 12, figs. 3-6. (Sterile and fertile, spores. Shensi, China.)
 1937 *Eboracia lobifolia* (Phillips): Brick, p. 35, pl. 10, figs. 2-4; text-fig. 16. (Sterile and fertile fragments. Central Asia.)
 1937 *Cladophlebis* (*Eboracia* ?) *lobifolia* var. *angustata* Brick, p. 37, pl. 10, fig. 1; text-fig. 17. (Sterile fragments. Central Asia.)

3. The following specimens are considered to be insufficiently characterised:

- 1877 *Alethopteris lobifolia* (Phillips) Feistmantel, p. 86, pl. 3, fig. 1. (Sterile, second pinnule not contracted. Jurassic; India.)
 1902 *Dicksonia lobifolia* (Phillips): Möller, p. 19, pl. 1, figs. 3-9; pl. 2, fig. 1. (Sterile pinnae, veins. Liassic; Bornholm. Literature.)
 1903 *Cladophlebis* cf. *lobifolia* (Phillips): Zeiller, p. 36, pl. 4, fig. 1, 1a. (Second pinnule not contracted. Rhaetic; Tonkin.)
 1905 *Cladophlebis heterophylla* Fontaine in Ward, p. 294, pl. 71, figs. 21-25. (Sterile, considered by some to be *lobifolia*, but second pinnule not contracted. Cretaceous; U.S.A.)
 1913 *Cladophlebis* cf. *lobifolia* (Phillips): Möller & Halle, p. 13, pl. 2, figs. 3, 4. (Small sterile fragments, veins. Lias; Sweden.)
 1914 *Cladophlebis lobifolia* (Phillips): Counillon, p. 1, pl. 1, fig. 1. (Obscure leaf. Indo-China.)
 1915 *Eboracia* (*Cladophlebis*) *lobifolia* (Phillips): Kryshtofovich, p. 95, pl. 3, figs. 4, 4a, 5, 5a. (Sterile fragments Amurland.)
 1922 *Cladophlebis* (*Eboracia*) *lobifolia* (Phillips): Yabe, p. 8, pl. 1, figs. 1-2; text-figs. 5, 6. (Imperfectly characterised fragments. Japan.)
 1924 *Cladophlebis lobifolia* (Phillips): Walkom, p. 81, pl. 15, fig. 2; text-fig. 2. (Details not clear in figure. Rhaetic; Queensland.)
 1925 *Cladophlebis* (*Eboracia*) *lobifolia* (Phillips): Kawasaki, p. 8, pl. 6, fig. 24. (Pinna fragment. Korea.)
 1931 *Cladophlebis lobifolia* (Phillips): Prinada, p. 14, pl. 1, fig. 5. (Fragment. Central Asia.)
 1933b *Cladophlebis* (*Eboracia*) *lobifolia* (Phillips): Sze, p. 68, pl. 8, figs. 2, 3; pl. 10, fig. 13. (Sterile fragments, basal pinnules mentioned but not clearly shown. Kansu, China.)
 1938 *Cladophlebis lobifolia* (Phillips): Oishi & Takahasi, p. 60, pl. 1, fig. 5, 5a. (Sterile fragments, basal pinnules obscure. Japan.)
 1940 *Cladophlebis* (*Eboracia* ?) *lobifolia* (Phillips): Oishi, p. 273, pl. 18, figs. 1-4. (Sterile, pinnules unusually short. Japan.)
 1957 *Eboracia lobifolia* (Phillips): Semaka, p. 333, text-figs. 18-23. (Sterile leaves. Lias; Roumania.)
 1957 *Eboracia lobifolia* (Phillips): Stanislavski, p. 37, pl. 3, figs. 6, 7. (Sterile leaves. S. Russia.)

EMENDED DIAGNOSIS. Lamina as a whole long-lanceolate. Sterile and fertile leaves probably similar. Estimated length of lamina 50-100 cm.; width up to 10-20 cm. in the middle region, reduced below and above. Petiole unknown. Rachis rather slender, upper surface broadly grooved, pinnae attached laterally, lower side rounded, nearly smooth but showing longitudinal cell striae, bearing minute hairs only. Pinnae arising at about 85° below, angle reduced to 50° above; typically arising at intervals of 1.5 cm. (1.0-2.0), but closer near the apex. Pinna as a whole slender, apex attenuated, width often slightly reduced in lower parts (but basal pinnules enlarged). Adjacent pinnae typically separated by small gaps below, rather closer and slightly overlapping above. Pinna rachis grooved above, under surface bearing minute hairs (hairs often lost). Branching katadromic throughout.

First pinnule on basiscopic side always broad, in middle region of large leaf basal pinnule forked into two blunt, diverging lobes. In upper and lower parts of large leaf, and throughout smaller leaves basal pinnules very broad but scarcely divided into two lobes. First pinnule on

acroscopic side in large leaf rather elongated and with a basal lobe projecting over the main rachis; first acroscopic pinnule only slightly modified in smaller leaves. Second and often third pinnules on both sides usually reduced in size and less lobed than later pinnules. Pinnules on basiscopic side of pinna rather longer and more acute than pinnules on acroscopic side. Largest pinnules (in middle region of largest leaves) typically 9×3 mm., margins waved,

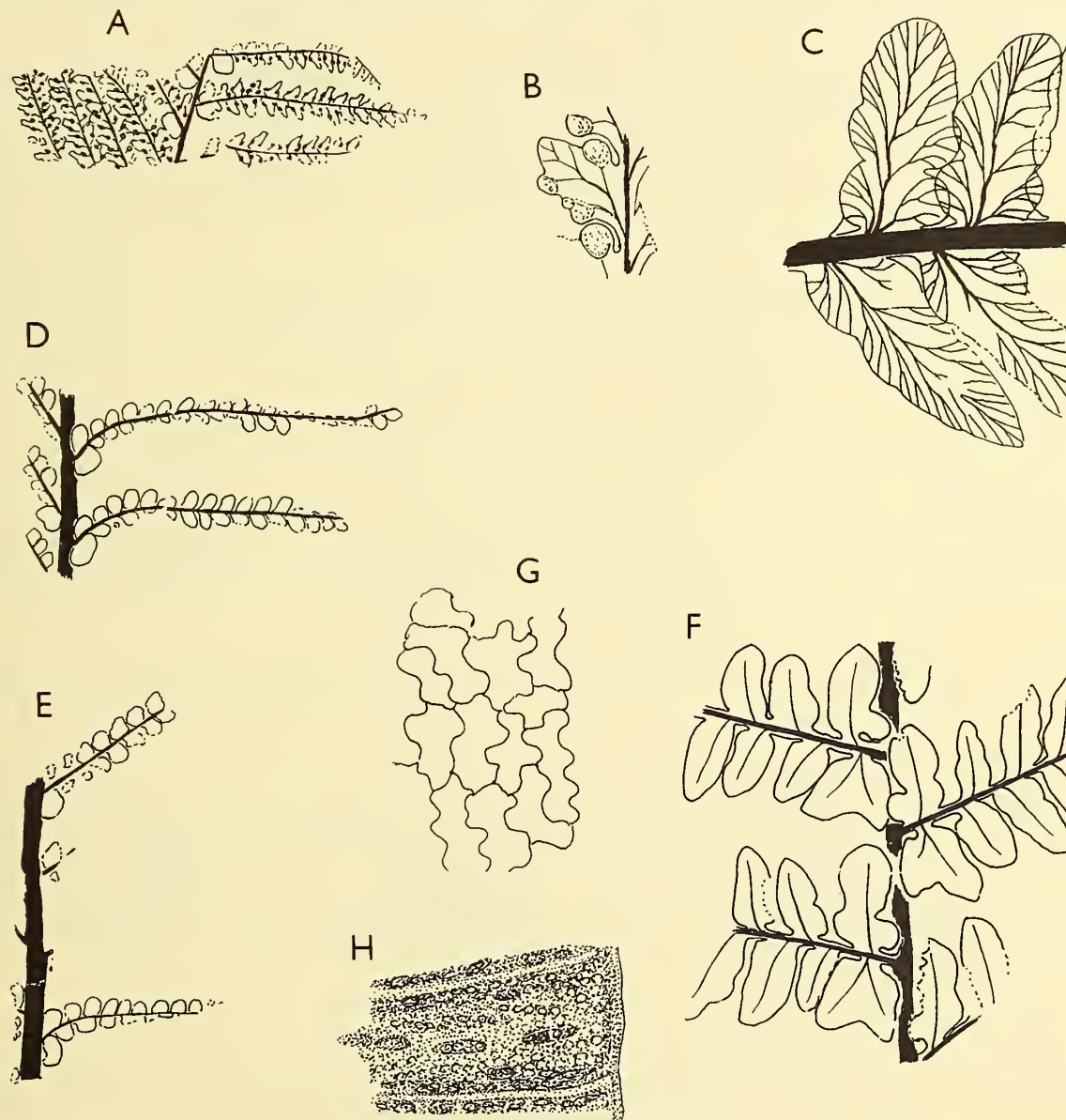


Fig. 62. *Eboracia lobifolia* (Phillips)

A, fertile specimen, Phillips Coll. J.5058, Oxford Museum of Geology, labelled '*P. inconstans* Phill. Stainton Dale', $\times 1$. B, details of a pinnule from A, $\times 4$. There is an obscure bulge above each sorus. C, large sterile pinnules showing asymmetry in both pinna and pinnule, V.32094, $\times 4$. D, E, two portions of Leeds City Museum specimen 16 labelled '*Neuropteris laevigata*, Lower Sandstone and Shale' (Unlocalised). D, is at 10 cm. above E, $\times 1$. F, part of rachis and pinnae of Leckenby specimen K.81, Sedgwick Museum, Cambridge, $\times 1$. (Another part was figured by Seward (1911), the rachis is 21 cm. long and the longest pinna about 12 cm.). G, epidermal cells in balsam transfer, V.32095, $\times 200$. H, two veins in lamina in transfer showing dark cells, V.32094, $\times 40$. C, G, H, are from the Gristhorpe Bed.

apex obtuse, base distinctly contracted on acroscopic side and slightly contracted on basisopic side. Towards apex of leaf pinnules smaller, relatively narrower and more acutely pointed, base scarcely contracted and margins entire. Towards base of leaf, pinnules smaller and more rounded, about 3×2 mm., margins entire. In smaller leaves pinnules smaller, entire, base only slightly contracted. In all leaves division between adjacent pinnules extending almost to the rachis but with a very narrow wing of lamina along the pinna rachis, but no wing along the main rachis.

VENATION. Branch veins arising in katadromic order. In largest pinnules midrib nearly straight, situated nearer basisopic margin and making an angle of 50° – 60° to the pinna rachis. First branch on basisopic side arising from pinna rachis rather than midrib; branches on basisopic side making a smaller angle to midrib and margins than branches on acroscopic side. Each main vein dividing up to three times, supplying a marginal lobe. In medium-sized pinnules midrib arising near basisopic margin and at an angle of about 30° to the rachis, and bending outwards to an angle of 45° , first basisopic branch arising near rachis. Lower veins forked twice. Ultimate branches reaching the margin at a concentration of 25–35 per cm.; intervals between pairs of veins often showing a vein-like mark. Lobed basal pinnules with an ill-marked midrib in each lobe.

Surface of pinnule convex, but margins not reflexed; substance rather dense.

Fertile pinnae like sterile, but fertile pinnules narrower and more pointed than sterile, margins sometimes strongly recurved. Sori 1–4 on each margin, always strongly recurved. Midrib giving off one unbranched vein to each sorus. Sorus with a solid base and prominent central placenta surrounded by a cylindrical indusium; whole sorus typically 0.6 mm. \times 0.4 mm. Indusium fairly robust. Sporangia numerous, shortly stalked, about 200μ long; annulus well developed, containing about 60 spores.

Spores rounded tetrahedral, sometimes with hollow sides, mean diameter 32μ , σ 6μ (range noted 24μ – 42μ). Triradiate crack long, with a strongly marked, thick border. Spore wall rather thick, smooth.

DISTRIBUTION. *E. lobifolia* is rather uncommon. It occurs in the Lower, Middle and Upper Deltaic. Most of the material is from the Gristhorpe Bed (Middle Deltaic), but there are also Lower Deltaic specimens from Haiburn Wyke and Roseberry Topping and from the Beast Cliff *Otozamites* Bed. Both fertile and sterile leaves occur together at Gristhorpe and Beast Cliff. The Upper Deltaic specimens are represented by minute fragments at Cambridge collected by Dr. M. Black from the Drifted Plant Bed in Burniston Wyke.

E. lobifolia is widespread in the Jurassic of Europe and Asia.

DISCUSSION. *Size of leaf.* All the better specimens suggest a bipinnate leaf, not a tripinnate one. No specimen is complete; the best (both sterile) are K.81, Leckenby Coll., Cambridge, a fragment about 23 cm. long from the middle and upper parts of a leaf about 20 cm. wide (see Seward 1911, pl. 7, fig. 73 for a photograph of part of it) and Leeds City Collection No. 16, a fragment 16 cm. long from the lower part of the lamina of a leaf only about 10 cm. wide. In both, the rachis tapers at about 0.5 mm. in 10 cm. This suggests that the Leeds specimen which has a rachis 2.5 mm. thick below, might be about 50 cm. long, but the broader Leckenby specimen may well be twice as long.

The fertile pinnules examined are all rather small, as are those figured by Raciborski. The fertile leaves seem, in general, to have had smaller pinnules than the sterile leaves.

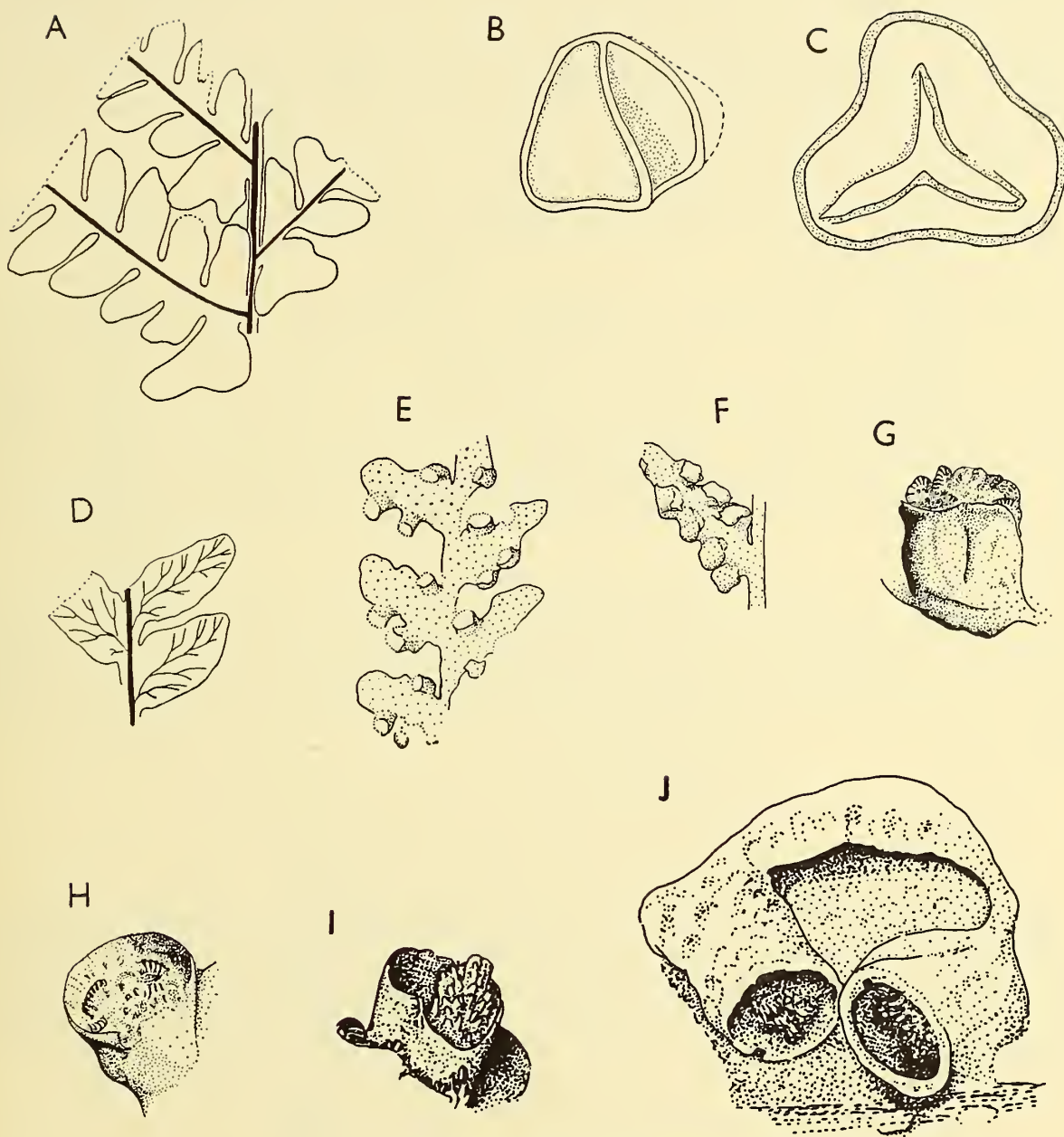


Fig. 63. *Eboracia lobifolia* (Phillips)

A, part of a sterile leaf (most of specimen omitted), V.31088, $\times 2$. B, C, spores, V.31092a, $\times 800$. D, small sterile pinnule showing venation, V.31091, $\times 4$. E, fertile pinnules in transfer showing sori (details omitted), V.31089, $\times 4$. F, fertile pinnule in transfer, V.31090, $\times 4$. G, H, two sori from the transfer shown in E; the indusium was broken in preparation in H, $\times 25$. I, transfer of sorus in which all the sporangia have fallen from the placenta, V.32096, $\times 25$. J, small fertile pinnule in transfer, the apex and sori are strongly incurved, V.32096, $\times 25$. All the specimens are from the Gristhorpe Bed, Cayton Bay.

A–H, are reproduced from Wilson & Yates (1953, text-fig. 3).

Structure of lamina. The sterile lamina is fairly thick and often almost opaque, but sometimes paler as a result of natural maceration. The veins are slender but often flanked by a rather broad sheath. The tissue between the veins sometimes shows a file of large oval cells, ? secretory or thick-walled (Text-fig. 62). Often no such cells are seen, but this may be the result of poor preservation. Where they are close and conspicuous they look like one of the *venuli recurrentes* of *Marattia anglica*. The mesophyll shows a number of small cells, but all very obscurely. The margin is reinforced by a band of thickened cells.

In a few specimens the maceration has proceeded further and nothing remains but the slender veins, a marginal band of fibres and some sinuous walled epidermal cells. Stomata were observed rather doubtfully.

COMPARISON. Fertile pinnae of *E. lobifolia* are quite distinct, particularly when transferred, but sterile leaves are less distinct. It was formerly supposed that the enlarged basal pinnule distinguishes them, but this is not so, *Dicksonia kendalli* having an exactly similar basal pinnule. However, in *D. kendalli* the second pinnule is not reduced as in *E. lobifolia*. Isolated fragments of sterile *E. lobifolia* are difficult to distinguish from *D. kendalli* and even from forms of *Todites williamsoni* and *Dicksonia mariopteris*. Such specimens have therefore been rejected in my own Collection and I am unwilling to identify them from the figures of others.

In a number of the better specimens from other regions, determined as *lobifolia*, the basal pinnule is developed typically, but the second pinnules are of normal size. These specimens are regarded as distinct and it is possible that some may be identical with *Dicksonia kendalli*. The excellent Polish leaves, however, agree fully with those from Yorkshire and their fertile leaves also look exactly similar, but as in Yorkshire leaves they only show the upper sides of their pinnules.

Subfamily DICKSONIEAE

Genus DICKSONIA L'Héritier

This genus is used here for fossils in which the sorus is broad and protected by an indusium of two equal, robust valves as in *D. antarctica*. The differences between *Dicksonia* and *Balantium* and *Cibotium* (formerly included in *Dicksonia*) are slight and not all related to features recognisable in leaf fragments but the fossils may be closer to the living *Dicksonia*. They are certainly *Dicksonia* in the old, comprehensive sense including these two as subgenera.

Dicksonia mariopteris Wilson & Yates

Text-figs. 64, 65

1953 *Dicksonia mariopteris* Wilson & Yates, p. 930, text-figs. 1, 2. (Figures and description repeated here.)

EMENDED DIAGNOSIS. Size of whole leaf unknown but for description assumed to be bipinnate or once pinnate with deeply pinnatifid pinnae. Shape of whole leaf not known. Leaf, as far as is known, wholly sterile or wholly fertile. In sterile leaf, pinnae arising at intervals of about 1.5 cm. in the upper part of leaf. (Main rachis scarcely known.) Pinna rachis exceeding 7 cm. in length, smooth, grooved above, rounded below, with a few simple hairs; hairs 1 cell wide but several cells long. Pinnules arising alternately in katadromic order, those on the basiscopic side often longer than the acroscopic ones. Typical pinnules about 11 mm. ×

4 mm., ovate, margins with rounded or irregular lobes, no marginal teeth present, acroscopic margin constricted, basiscopic margin scarcely constricted. Apex obtuse or rounded. Adjacent pinnules separated by gaps but connected along the pinna rachis by a very narrow web of lamina. Pinnules towards pinna apex becoming more acute and triangular. Lowest basiscopic pinnules modified, typically enlarged, stalked and divided into three lobes. Second and third

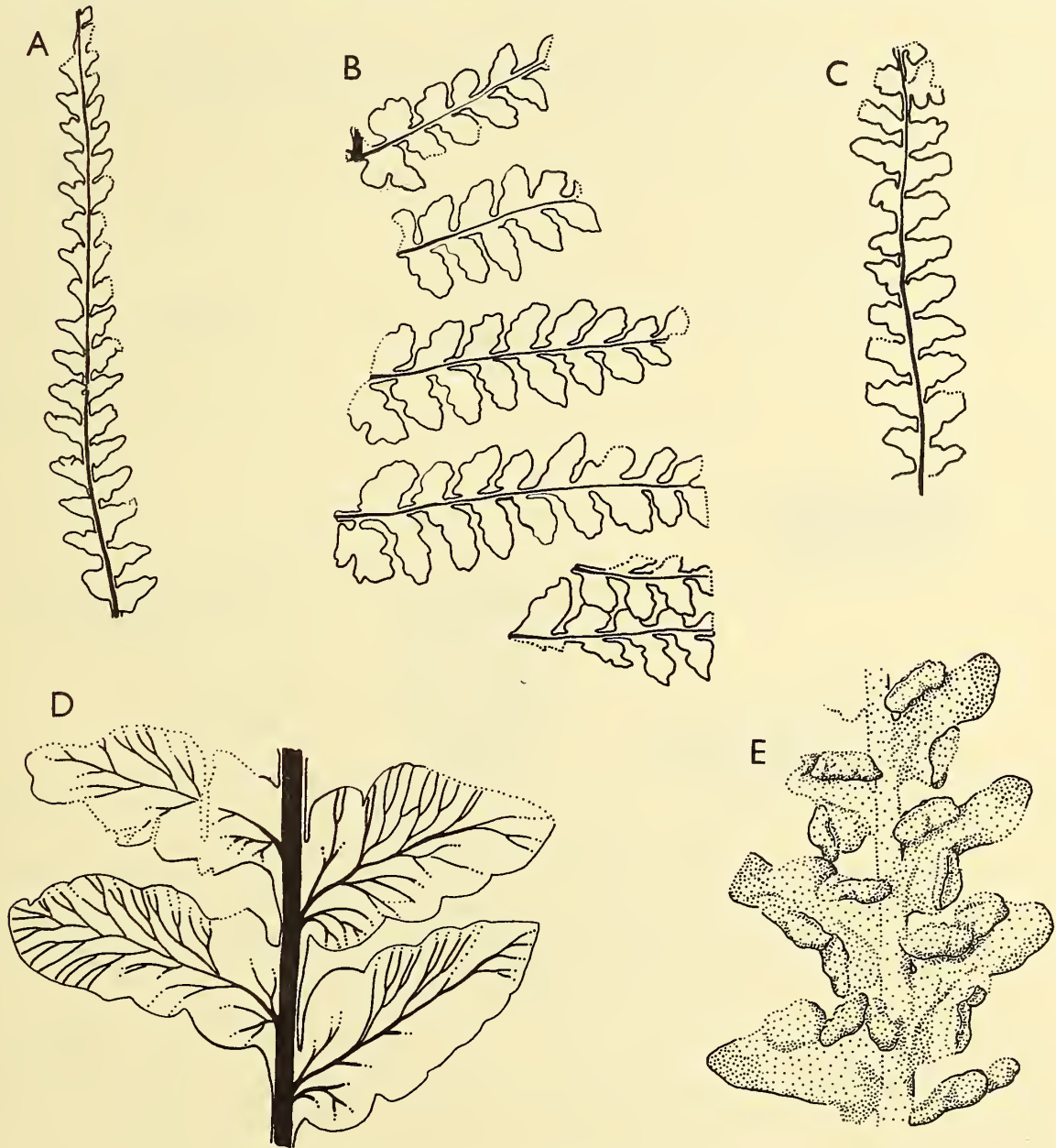


Fig. 64. *Dicksonia mariopteris* Wilson & Yates

A, holotype, fertile pinna, V.31075, $\times 1$. B, upper part of sterile leaf. Specimen in Leeds City Museum, $\times 1$. C, sterile pinna, V.31074, $\times 4$. D, venation of sterile pinnules, V.31074, $\times 4$. E, transfer preparation of fertile pinna, V.31076, $\times 4$.

All the figures are from Wilson & Yates (1953, text-figs. 1, 2). B, is unlocalised, the rest are from Beast Cliff *Equisetum* Bed.

pinnules not all reduced in size. Margins of pinnules slightly recurved. Substance of lamina rather thick and veins obscurely shown. Midrib arising at about 45° to the rachis and bending outwards at first nearer basiscopic margin but becoming median. Branching katadromic. First basiscopic vein arising near or on the pinna rachis. Lower veins forking three times and branches supplying a lobe; final branches reaching the margin at a concentration of about 24 per cm.

Fertile pinna as large as sterile, and resembling it except that the pinnules are narrower; sterile parts of pinnules as in sterile leaf. Sori one to about five, borne laterally on both sides of a pinnule, strongly recurved. Venation and lamina as in sterile pinnule but with a single unbranched vein supplying each sorus.

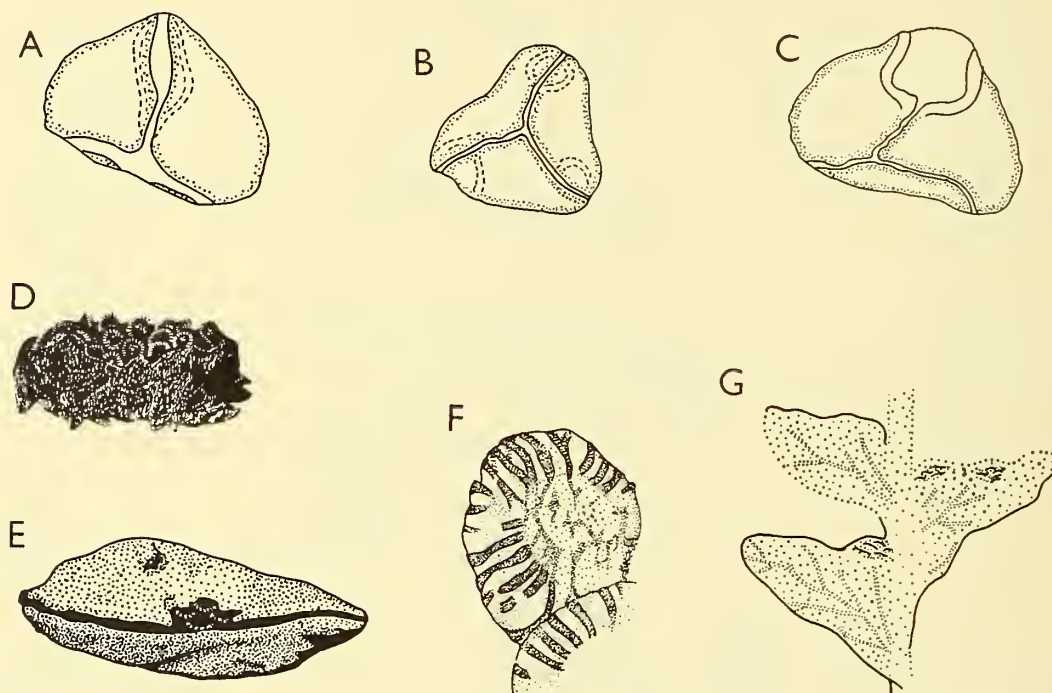


Fig. 65. *Dicksonia mariopteris* Wilson & Yates

A–C, spores, all slightly distorted, V.31079, $\times 800$. D, isolated placenta of sorus, indusia removed but some sporangia present, V.31077, $\times 25$. E, sorus as seen in transfer, V.31078, $\times 15$. F, sporangium showing part of annulus, V.31077, $\times 200$. G, small fertile pinnules from above showing soral veins, V.31075, $\times 4$. All figures are from Wilson & Yates (1953, text-fig. 2).

All specimens are from Beast Cliff *Equisetum* Bed.

Sorus broadly oval, compressed, length (measured along pinna margin) typically 2.5 mm. (2–3 mm.) thickness (indusium to indusium) 0.75 mm.; height about 1 mm. Indusium robust, composed of two similar valves, outer edges entire, normally pressed together. Sporangia numerous, about 200μ wide, of varied age in one sorus. Annulus well developed, ? complete; stalk short. Spores rounded triangular to triangular, mean width 39μ , $\sigma 8\mu$, range noted 24μ – 56μ . Triradiate cracks rather long with a slightly thickened margo. Wall fairly thick, smooth.

DISTRIBUTION. Apart from the unlocalised Leeds specimen *D. mariopteris* occurs only in the Middle Deltaic Gristhorpe Bed and in the Lower Deltaic Beast Cliff *Equisetum* Bed where it is locally common. Its determination, when sterile, in the Gristhorpe Bed is difficult because

a lobed form of *Todites williamsoni* occurs with it, but there is a specimen (39258) which though imperfectly localised is in a matrix similar to that of the Gristhorpe Bed.

DISCUSSION. *D. mariopteris* is rare and no additional specimens are known. All specimens are pinna fragments apart from the one shown in Text-fig. 65. Sterile and fertile fragments are equally common. Wilson & Yates note that the sori are scarcely seen till transferred and that the indusia are normally pressed together. The sporangia were mostly ripe but undehiscent and they failed to count the spore output per sporangium to their satisfaction; nor could they decide finally whether the annulus continued past the stalk. They also note the frequent presence of loop-like folds in the spore wall; these are no doubt creases produced in compression but they do seem specially prevalent in this species.

The sterile and fertile fragments were identified because (1) they are associated in both localities, and in one (the *Equisetum* Bed) there is no other fern resembling it; (2) the fertile leaf produces transitional pinnules.

COMPARISON. No fossil is known which has fertile pinnules like those of *D. mariopteris*, but the sterile pinnules are less distinct. The basal pinnules are enlarged but rather differently from those of *Eboracia lobifolia* and *D. kendalli*, another difference from *E. lobifolia* is that the second pinnule is not reduced.

It is difficult to separate fragments of the largest and most lobed form of *Todites williamsoni* from *D. mariopteris*. One difference, however, is that the lamina is of thinner substance and flatter, and the veins are easier to see in *T. williamsoni*. Wilson & Yates suggested that the fragment figured by Seward (1900, text-fig. 21) might belong to *D. mariopteris*, but it is more likely that this (and text-fig. 20 also) are *T. williamsoni*.

Certain forms of the Asiatic *Cladophlebis gigantea* with lobed pinnules (e.g. P'an, 1936, pl. 7, fig. 1) approach *D. mariopteris* but differ in their basal pinnules.

Dicksonia kendalli sp. nov.

Text-fig. 66

DIAGNOSIS. (Size of whole leaf unknown, but for description assumed to be once pinnate with pinnatifid pinnae, or almost bipinnate.) Leaf sterile or almost wholly fertile, but sterile and fertile leaves similar. Pinnae arising at intervals of about 12 mm., decreasing above, length of pinna about 8 cm., width remaining uniform for a considerable distance. Main rachis smooth rather slender, rounded below, with a broad groove above, pinna rachis similar. (Bristles absent, hairs not observed.) Pinnules arising alternately, the first being on the basiscopic side; pinnules on the two sides of equal size. First basiscopic pinnule very broad, usually sterile even in fertile leaf; first pinnule on acroscopic side also somewhat broad. Second and third pinnules in sterile leaf not reduced, these and later pinnules ovate, about 3 mm. \times 2 mm. Typical sterile pinnules in contact with their neighbours, margins entire, not recurved, apex rounded, base unconstricted, substance of lamina moderately thick, veins somewhat prominent. Midrib arising at an angle of about 30° and bending outwards, order of branching strongly katadromic with the first basiscopic vein arising from the pinna midrib. Lateral veins forked once or twice, ultimate branches reaching margin at a concentration of about 16 per cm.

Fertile pinnules with a reduced lamina, each bearing a single large sorus on the first acroscopic vein. Sorus not recurved but lying in the horizontal plane, shape broadly oval to reniform, width up to 2.5 mm., height (base to free margin) up to 1.5 mm. (thickness not known).

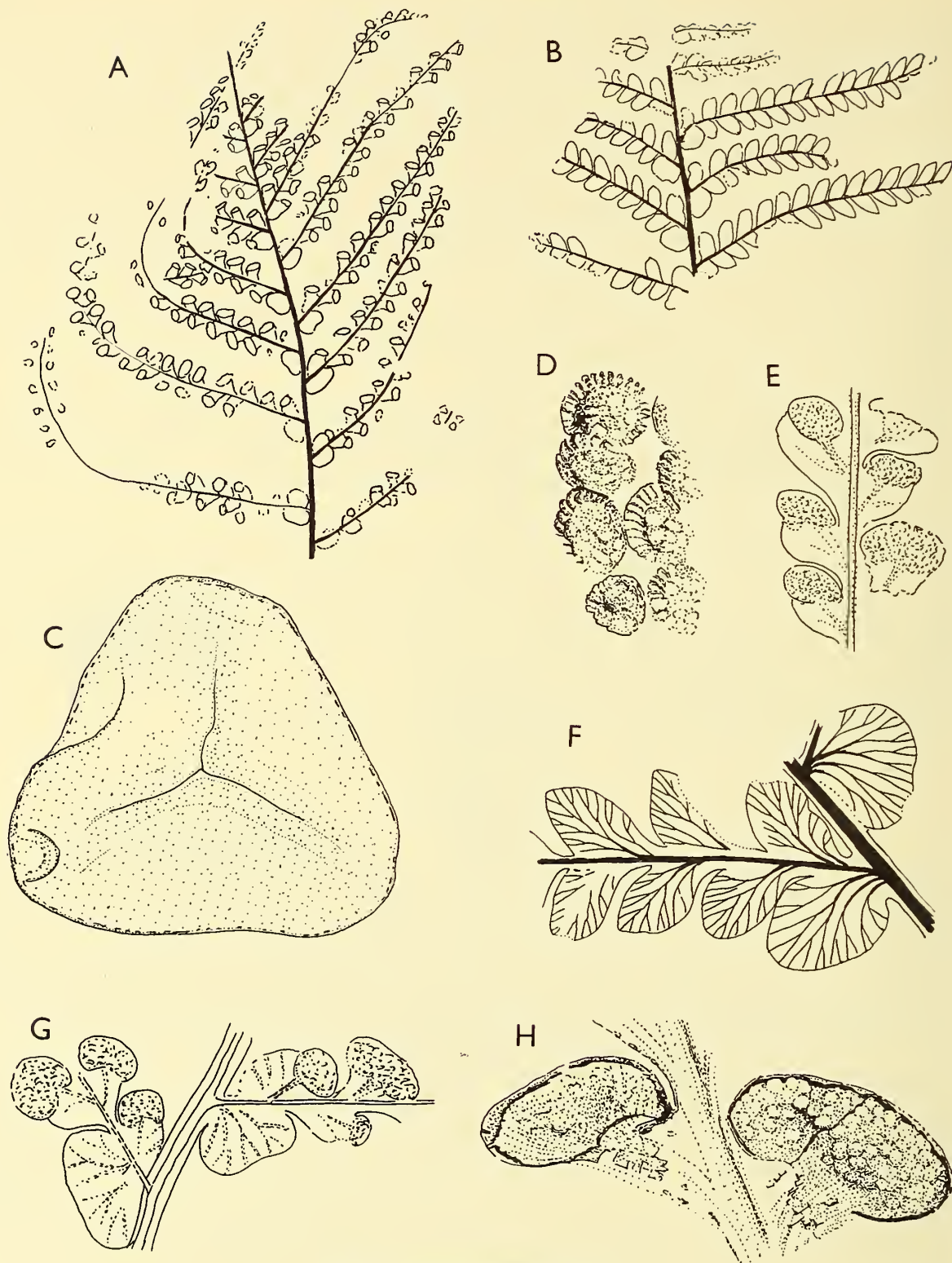


Fig. 66. *Dicksonia kendalli* sp. nov.

A, fertile leaf, holotype, V.32252, $\times 1$. B, top of sterile leaf, V.32253, $\times 1$. C, spore from A, $\times 800$. D, sporangia from one of the sori in A, $\times 50$. E, upper sori from A, $\times 4$. F, venation from B, $\times 4$. G, lower sori from counterpart of A, $\times 4$. H, two sori from A, that on the left with, that on the right without its indusium. The crack around the sori is caused by shrinkage, $\times 10$.

Both specimens are from Roseberry Topping.

Indusium composed of two similar valves; valves moderately robust, smooth, outer edges entire and pressed together.

Sporangia numerous, about 300μ wide; annulus well developed. Spores rounded-triangular (sides more often convex than concave) mean diameter 67μ , σ 5.5μ , range noted 58μ – 78μ . (A few very small spores were excluded.) Triradiate crest rather prominent, margo broad but very ill-marked. Spore wall not very thick, almost smooth.

HOLOTYPE. V.32252.

DISTRIBUTION. *D. kendalli* is only known from Roseberry Topping, a locality near the base of the Lower Deltaic.

DISCUSSION. There are only two specimens of *D. kendalli*, both are figured here. The holotype (fertile) has both part and counterpart. They are preserved in a fine-grained shale which has undergone some recent oxidation and the coaly substance has contracted. This has caused a crack to develop around the sori but no other marked effects. The majority of the sori show no distinct sporangia but are covered by a continuous membrane, the indusium; its cells are obscure. This looks to be equally developed on the two sides and the whole sorus lies almost in the horizontal plane. A few sori show the sporangia very clearly, presumably because the indusium is missing and as the indusium is not seen on the counterpart it must have been lost before preservation.

The sterile leaf is attributed to this species because of its association and great similarity to the sterile parts of the fertile leaf.

COMPARISON. *D. kendalli* differs from *D. mariopteris* in having a single sorus on each pinnule instead of several. The sterile pinnules are smaller and less lobed.

The spores of the two differ in mean size (*D. mariopteris*, 39μ ; *D. kendalli*, 67μ .)

Gonatosorus nathorsti Raciborski (1894) and Prinada (1938) agrees in the single sorus on each pinnule but differs in its much smaller size. Microscopic details are not available. *Gonatosorus sphenopteroides* Brick (1937) more closely resembles *Coniopteris margaretae* but again no microscopic details are known.

The sterile leaf of *D. kendalli* is almost exactly like that of *Eboracia lobifolia*; the only difference being that the second basiscopic pinnule in *D. kendalli* is not reduced, a character of unproved constancy. The fertile leaf differs considerably in its single large sorus on each pinnule, the flat instead of tubular shape of the sorus and in its larger spore.

Dicksonia kendalli is named after its collector, Miss M. W. Kendall.

Family ASPIDEAE?

Genus ASPIDISTES nov.

DIAGNOSIS. Leaf repeatedly pinnate, ultimate pinnules with a midrib and diverging branch veins. Branching katadromic throughout. Sterile and fertile leaves similar.

Sori borne on the under surface of the lamina on a forward-pointing vein; round, covered by a rounded indusium, indusium attached centrally or near the midrib. Sporangia lens shaped, probably of mixed ages, stalked, usually falling after dehiscence; annulus well developed, approximately vertical, probably incomplete; sporangium producing 48 spores. Spores triangular, scar triradiate; wall smooth, without perispore.

TYPE SPECIES. *Aspidistes thomasi* sp. nov.

DISCUSSION. The name is from *Ασπιδιστής* a shield-bearer and refers to the indusium. *Aspidistes* is the oldest fern known to me with an aspidioid sorus and it agrees in most respects with *Aspidium* (*sensu lato*) particularly in its *indusium superum*. It differs in its katadromic branching (but this may not be important) and in its spore. So far as I know the modern Aspidaceae have wedge-shaped spores with a perispore, while *Aspidistes* has a triangular spore without perispore as in most 'primitive' ferns. Bower (1923: 260) belittles the taxonomic value of the spore form but others rate it more highly—though admitting that it is occasionally anomalous. The palaeobotanist, with fewer characters available will naturally consider it seriously.

Bower (1928: 114, 128) regarded the *indusium superum* of *Polystichum* as advanced among the Aspidaceae or Dryopteroid ferns. I have no view on this subject, but the occurrence of an aspidioid sorus as early as the Middle Jurassic is disturbing. It may be that these 'advanced' ferns had already evolved but were living in the background (as is often held for the angiosperms). It may also be that Aspidaceae were evolving actively in the Jurassic but the course of soral evolution was not as Bower supposed. It may also be that *Aspidistes* is not a member of the Aspidaceae at all (as is indeed suggested by its spore) but merely an interesting and early imitation from another stock.

Aspidistes thomasi sp. nov.

Text-figs. 67, 68

?1834 *Pecopteris Murrayana* Brongniart in part, pl. 126, fig. 5, 5a only.

?1875 *Sphenopteris Murrayana* (Brongn.) Phillips in part, p. 212, lign. 26, as above.

DIAGNOSIS. (Form of whole leaf unknown, available fragments regarded as primary pinnae). Sterile and fertile pinnae similar; width 3–6 cm., pinna rachis slender, deeply channelled above, rounded below, without hairs. Secondary pinnae arising at intervals of about 1 cm. and at an angle of about 60°, straight or curving forwards, tapering gradually from base to apex. First pinnule (tertiary branch) arising close to the rachis on the basiscopic side (katadromic branching), later ones usually alternate. Lower pinnules on acroscopic side usually longer than those on basiscopic side, upper ones equal. Basal pinnules unspecialised, lower ones almost at right angles to their rachis, but upper ones arising at about 60°. Pinnules up to 7 mm. × 2.5 mm., but often smaller; in larger pinnules margins indented to form rounded lobes, lobes tending to alternate katadromically; first acroscopic lobe larger than first basiscopic lobe. Apex of pinnule rounded. In smaller pinnules margin more or less entire. Substance of lamina fairly thick, margins curved downwards; upper surface smooth, lower surface bearing numerous scattered, apparently sessile, unicellular glands. Midvein fairly broad, straight, laterals arising in katadromic order to supply the lobes, lower ones forked once or twice.

Fertile pinnules similar to sterile, but margins often more strongly recurved, therefore appearing narrower and wider spaced. Sori in larger pinnules one in middle of each lobe, in smaller pinnules in a row on each side of midrib; largest pinnule bearing up to 8 sori. Sori typically about 1.0 mm. wide, almost in contact, each partly covered with a rounded indusium about 0.6 mm. wide. Substance of indusium rather robust but margins delicate, showing radiating cells and bearing a few glands in the middle; margins bending back at maturity except at the point nearest the midrib. Sorus borne on the end of a forward-pointing branch vein.

Sporangia about 200μ wide with about twelve thickened cells in the annulus and containing

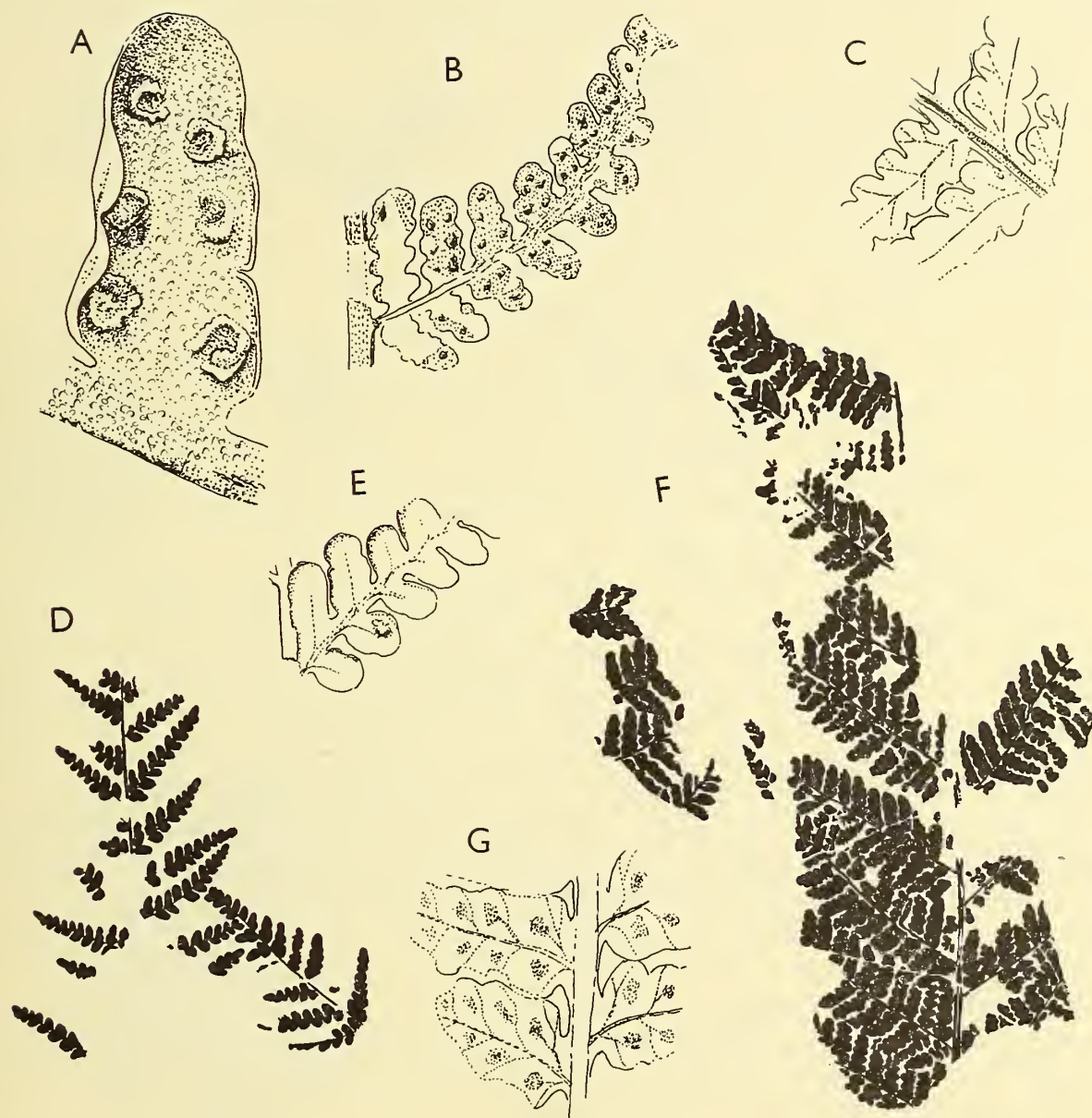


Fig. 67. *Aspidistes thomasi* sp. nov.

A, fertile pinnule in transfer, showing reflexed margins and indusia. Nearly all sporangia have fallen, V.32258, $\times 20$. B, one secondary pinna showing sori, V.32259, $\times 4$. C, details of pinnules from near top of F, $\times 4$. D, holotype (left), and an associated fertile pinna. Another further on the left is omitted, V.32255, $\times 1$. E, secondary pinna from holotype, seen from above. Only one sorus is visible, $\times 4$. F, sterile specimen showing fragments of two primary pinnae, V.32256, $\times 1$. G, secondary pinna from Beast Cliff, *Otozamites* Bed, V. 32257, $\times 4$.

All specimens (except G) are from the Gristhorpe Bed, Cayton Bay.

48 spores. Spores triangular, mean diameter 35μ , σ 4μ (widest and narrowest observed 45μ and 29μ); triradiate crack rather long, often slightly sinuous, border thickened. Spore wall rather thick, smooth. Named after Dr. H. Hamshaw Thomas who collected most of the material.

HOLOTYPE. V.32255.

DISTRIBUTION. *Aspidistes thomasi* is represented by several small specimens from the Gristhorpe Bed, Cayton Bay, and one fragment from the Beast Cliff *Otozamites* Bed.

DISCUSSION. Most of the specimens are fertile, but the plane of cleavage rarely exposes the sori. It either passes above the lamina, or between the lamina and the sorus. Their study was thus impossible until the transfer method was available.

The sterile specimens were identified with the fertile because of their close agreement in form, and in the glandular hairs of the under side.

There is nothing to show the size of the leaf; the fragments described as primary pinnae could be secondary pinnae, or even whole leaves. They show numerous transitions in the lobing of the pinnules and a large lobed pinnule from below is very like a secondary pinna from the upper part of the same fragment. The sori vary in number with the size of the pinnule, the longest having 6–8, each in its own lobe, smaller ones with faintly lobed margins having 4–5 in rows alongside the midrib, and the smallest being rounded and with only 1–2 sori and thus very like a lobe of a larger pinnule.

The spores are rather characteristic, being small and almost all having hollow sides when compressed vertically (often more hollow than in the one figured). Folds caused in compression are very commonly present towards the corners. There is some evidence that the numerous sporangia ripened at different times. In one specimen where the sporangia have dehisced and fallen off, only a few empty ones remain. There are also many small and probably abortive sporangia of different sizes. This is consistent with continued formation of new sporangia. V.32261 is the only specimen with numerous ripe sporangia, and only a bit of one sorus was macerated. This gave five sporangia with separate spores and one, thought to be younger, with coherent spores. There was no evidence of still younger sporangia. The spore counts were made from this specimen; the best being 42, 49, 50. Assuming that a few spores were lost from the 42 and that in the 49 and 50 a few broken spores were counted as whole ones, the typical spore number is 48.

Although many sporangia show annulus cells in their outer parts, no good view of a sporangium base was seen. There are several specimens which suggest that the annulus passes up one side, over the top and half way down the other side, just as in most Polypodiaceae. In some small and ill-formed sporangia it appears that the annulus ceases at the stalk, but this is not conclusive.

The indusium is persistent and seems to be robust. In V.32261 it appears to be attached more or less centrally, but in most specimens, where the sporangia have fallen, the margins are curled back except usually on the edge nearest the midrib, so that it forms a letter C. This suggests a form intermediate between the perfectly round and centrally attached indusium (as in *Polystichum setiferum*) and the heart-shaped one (as in *Dryopteris filix-mas*). In *Aspidistes* the sporangia appear less numerous on the side near the midrib.

The structures termed unicellular glands on the under-surface consist of very delicate brownish bodies exposed when the specimen is transferred (Text-fig. 68 B). Usually they have the appearance of a burst blister, being a hemispherical dome with a large hole in the roof.

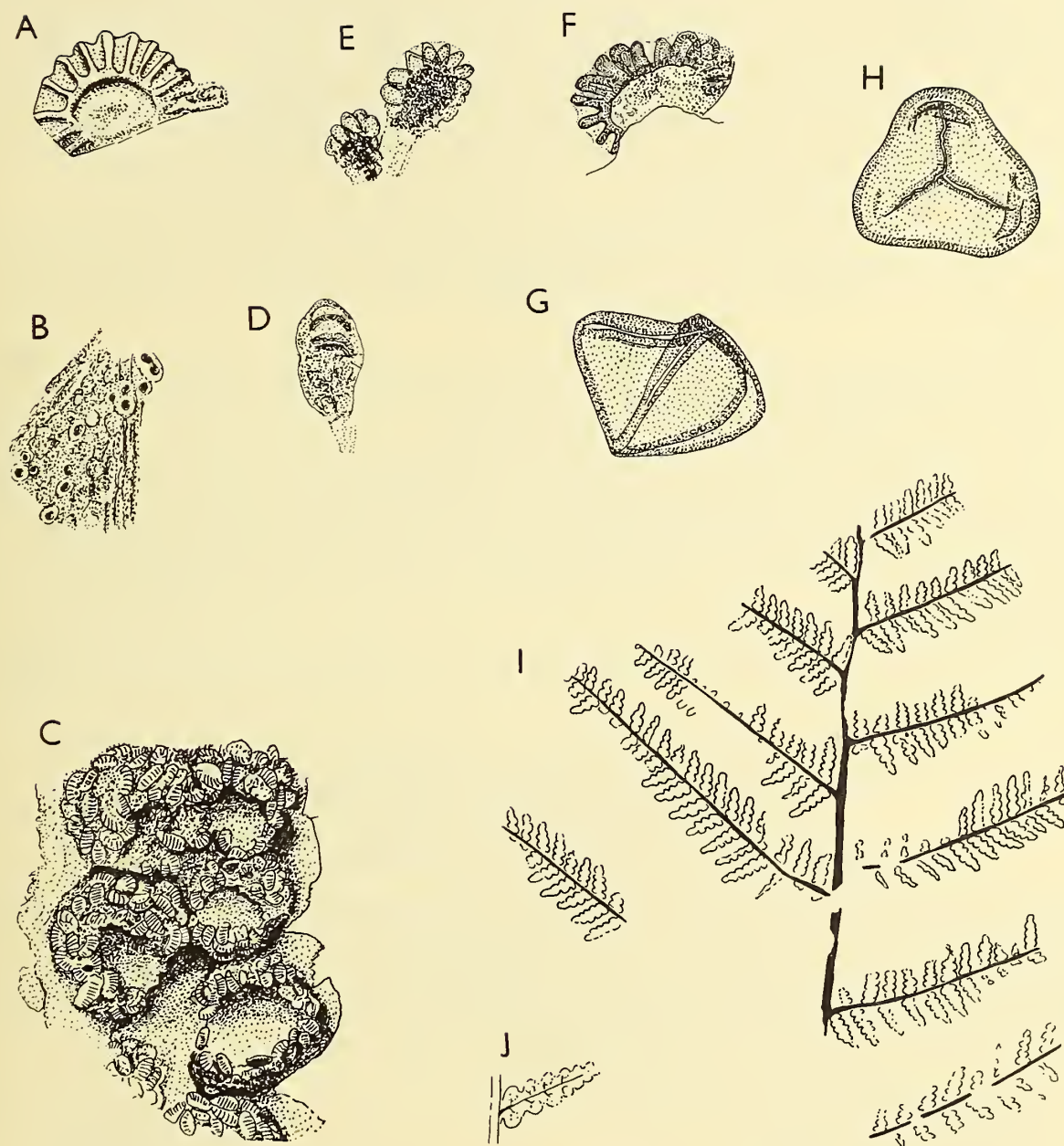


Fig. 68. *Aspidistes thomasi* sp. nov.

A, empty sporangium by reflected light, from transfer preparation, V.32260, $\times 100$. B, under surface of fertile pinna in transfer showing blister-like glands, from holotype, V.32255b, $\times 100$. C, fertile pinna in transfer, V.32261, $\times 20$. D, E, small abortive sporangial remains on old sori, by transmitted light, V.32255, $\times 100$. F, empty sporangium, by transmitted light, V.40257, $\times 100$. G, H, spores, V.32262, $\times 800$. I, leaf in Yorkshire Museum, in Gristhorpe type of matrix (? fertile), $\times 1$. J, details from I. There is a hole in the middle of each lobe, $\times 2$. A-H, are from the Gristhorpe Bed, Cayton Bay.

A search through some Recent ferns revealed similar looking organs on the 'golden fern', *Cheilanthes argentea* var. In a dried leaf of this fern the whole under-surface is crusted with a yellow secretion, when this is dissolved in alcohol the collapsed glands look very similar. *Cheilanthes*, however, has very different sori and is usually placed in the Gymnogrammeoideae. Two less familiar species of the Dryopteridoideae are *Cyclosorus glandulosus* (Bl.) Ching, with similar-looking but less frequent scattered glands, and *Thelypteris viscosus* (L. Sm.) Ching, with glands on the veins. I owe thanks to Dr. R. E. Holttum for this information and for pieces of each of these Malayan ferns.

COMPARISON. No fossil has been described from the Mesozoic which at all resembles the fertile fragments of *Aspidistes thomasi*, but the sterile fragments are very like those of several species, particularly *Kylikopteris arguta* and *Klukia exilis* in Yorkshire. Differences from *K. arguta* are:

In a similar sized pinna the rachis is broader and less channelled above. In similar sized pinnules the base is more contracted and its vein branches are more crowded. The lamina is less convex above and has no glandular covering below.

Klukia exilis rarely has such blunt pinnules with rounded lobes. The under-surface of the lamina is densely hairy instead of being thinly covered with glands.

Coniopteris murrayana is occasionally similar in the rounded lobes of its pinnules, but the pinnules are triangular rather than oblong in shape. Its margins are flat, and the under side is not glandular.

There must be many supposedly sterile leaves in other floras which look rather like *A. thomasi*, but comparison is of little value since it is the sorus which makes this leaf determinable.

Unclassified Ferns

Form-Genus CLADOPHLEBIS Brongniart, 1849 : 105

There are twelve species of Yorkshire Jurassic ferns with more or less Pecopterid pinnules, most of which in the sterile state are usually included in *Cladophlebis*. Ten of these are, however, placed in other genera in this work according to the form of the fertile leaves, but are included in the key given below. This key only attempts to separate the more typical specimens and would fail with fragments from the extremities of a leaf.

- | | |
|---|------------------------------|
| (1) Pinnules sharply toothed | 2 |
| Pinnule margin entire or with rounded lobes | 3 |
| (2) Base of pinnule contracted | <i>Todites thomasi</i> |
| Base of pinnule uncontracted | <i>Todites denticulatus</i> |
| (3) Lateral veins in middle of pinnule forked twice or more | 4 |
| Lateral veins simple or once forked | 10 |
| (4) Lower lateral veins forked 3 times | 5 |
| Lower lateral veins forked twice | 8 |
| (5) Basal pinnules unspecialised | 6 |
| Basal pinnules specialised | 7 |
| (6) Branching of leaf and veins katadromic | <i>Todites williamsoni</i> |
| Branching of leaf and veins anadromic | <i>Todites princeps</i> |
| (7) Basal pinnule very broad or forked | <i>Eboracia lobifolia</i> |
| Basal pinnule elongated, lobed | <i>Dicksonia mariopteris</i> |

- | | | | |
|------|---|----------------------------------|----|
| (8) | Pinnules ovate | <i>Dicksonia kendalli</i> | |
| | Pinnules elongated | | 9 |
| (9) | Pinnæ opposite, all rachises slender | <i>Cladophlebis haiburnensis</i> | |
| | Pinnæ alternate, rachises stout | <i>Cladophlebis aktashensis</i> | |
| (10) | Branching anadromic | <i>Todites princeps</i> | |
| | Branching katadromic | | 11 |
| (11) | Rachises slender, branching sparse | <i>Klukia exilis</i> | |
| | Rachises stout, branching crowded | | 12 |
| (12) | Pinnule margins flat, underside smooth | <i>Kylikopteris arguta</i> | |
| | Pinnule margins recurved, underside glandular | <i>Aspidistes thomasi</i> | |

Cladophlebis haiburnensis (L. & H.) Brongniart

Text-fig. 69

1. Yorkshire specimens.

- 1836 *Pecopteris haiburnensis* Lindley & Hutton, p. 97, pl. 187. (Leaf fragment, only shown roughly.) Holotype in Hancock Museum, Newcastle.
- 1849 *Cladophlebis haiburnensis* (Lindley & Hutton) Brongniart, p. 105. (Name.)
- 1875 *Pecopteris haiburnensis* L. & H.: Phillips, p. 211, lign. 25. (Sketch.)
- 1900 *Cladophlebis haiburnensis* (L. & H.): Seward, p. 150. (Brief notes only.)
- 1907 *Cladophlebis haiburnensis* (L. & H.): Seward, pp. 24 (English), 26 (Russian); pl. 2, fig. 34 only. (Pinnule of specimen in Sedgwick Museum. Russian material probably distinct.)
- 1911 *Cladophlebis haiburnensis* (L. & H.): Seward & Thomas, pp. 3, 14, text-fig. 1 only. (Drawings of holotype. Russian material probably distinct.)
- 1947 *Cladophlebis haiburnensis* (L. & H.): Frenguelli, p. 30, text-fig. 18. (Figure from Lindley & Hutton; discussion.)

2. Specimens from other regions.

- 1925 *Cladophlebis haiburnensis* (L. & H.): Kawasaki, p. 18, pl. 5, figs. 16–20; pl. 6, figs. 21, 22. (Fragments only, but see Kawasaki, 1926, 1939. Lias; Korea.)
- 1926 *Cladophlebis haiburnensis* (L. & H.) forma *aquilina* Kawasaki, p. 3, pl. 2, figs. 4–6; pl. 3, fig. 10. (Lias; Korea.)
- 1931 *Cladophlebis ingens* Harris, p. 55, text-fig. 17 A–D. (Lower Lias; E. Greenland.)
- 1931 *Cladophlebis* sp. 'a', Harris, p. 56, text-fig. 19. (Lower Lias; E. Greenland.)
- 1939 *Cladophlebis haiburnensis* (L. & H.): Kawasaki, p. 12, pl. 2, fig. 9; pls. 3, 4; text-fig. 2. (Lias; Korea.)

3. Specimens referred to *C. haiburnensis* but considered either distinct or else indeterminable.

- 1894 *Thinnfeldia*(?) *haiburnensis* (L. & H.) Raciborski, p. 209, pl. 20, figs. 3–6. (Fragments. Veins rather different, perhaps a true *Thinnfeldia*. Upper Lias; Poland.)
- 1905 *Cladophlebis haiburnensis* (L. & H.): Ward, p. 71, pl. 11, figs. 8–10. (Indeterminable fragments. Jurassic; Oregon.)
- 1907 *Cladophlebis haiburnensis* (L. & H.): Seward, pp. 24, 26, pl. 4, fig. P; pl. 6, figs. 35, 41. (Distinct, rachis thicker, pinnæ at smaller angle. Turkestan.) Pl. 2, fig. 34 is a British specimen.
- 1910 *Cladophlebis haiburnensis* (L. & H.): Kryštofovich, p. 6, pl. 1, figs. 2, 3. (Indeterminable fragments. Ussuriland.)
- 1911 *Cladophlebis haiburnensis* (L. & H.): Seward & Thomas, pp. 3, 14, pl. 1; pl. 2, figs. 7, 8; pl. 3. (Distinct, rachis thicker, pinnæ at smaller angle, crowded. Irkutsk. Figs. 1, 1 A holotype, Yorkshire.)
- 1911 *Cladophlebis haiburnensis* (L. & H.) Thomas, pp. 17, 65, pl. 3, figs. 4–6a. (Distinct, pinnæ alternate. Russia.)
- 1912 *Cladophlebis haiburnensis* (L. & H.): Seward, p. 19, pl. 2, figs. 31–35. (Indeterminable fragments. Afghanistan.)
- 1912a *Cladophlebis haiburnensis* (L. & H.): Seward, pp. 10, 26, pl. 1, fig. 7, 7a; pl. 2, fig. 10, 10a. (Distinct, pinnæ crowded, alternate; pinnules small. Amurland.)
- 1922 *Cladophlebis haiburnensis* (L. & H.): Yabe, p. 16, pl. 2, figs. 9–11; text-figs. 12–16. (More like *C. aktashensis*. Korea, Japan, China.)
- 1927 *Cladophlebis haiburnensis* (L. & H.): Kryštofovich, p. 560, pl. 31, figs. 3, 4. (Indeterminable fragments. Siberia.)
- 1928 *Cladophlebis haiburnensis* (L. & H.): Makarewiczówna, p. 12, pl. 13, fig. 5. (Indeterminable fragment. Poland.)

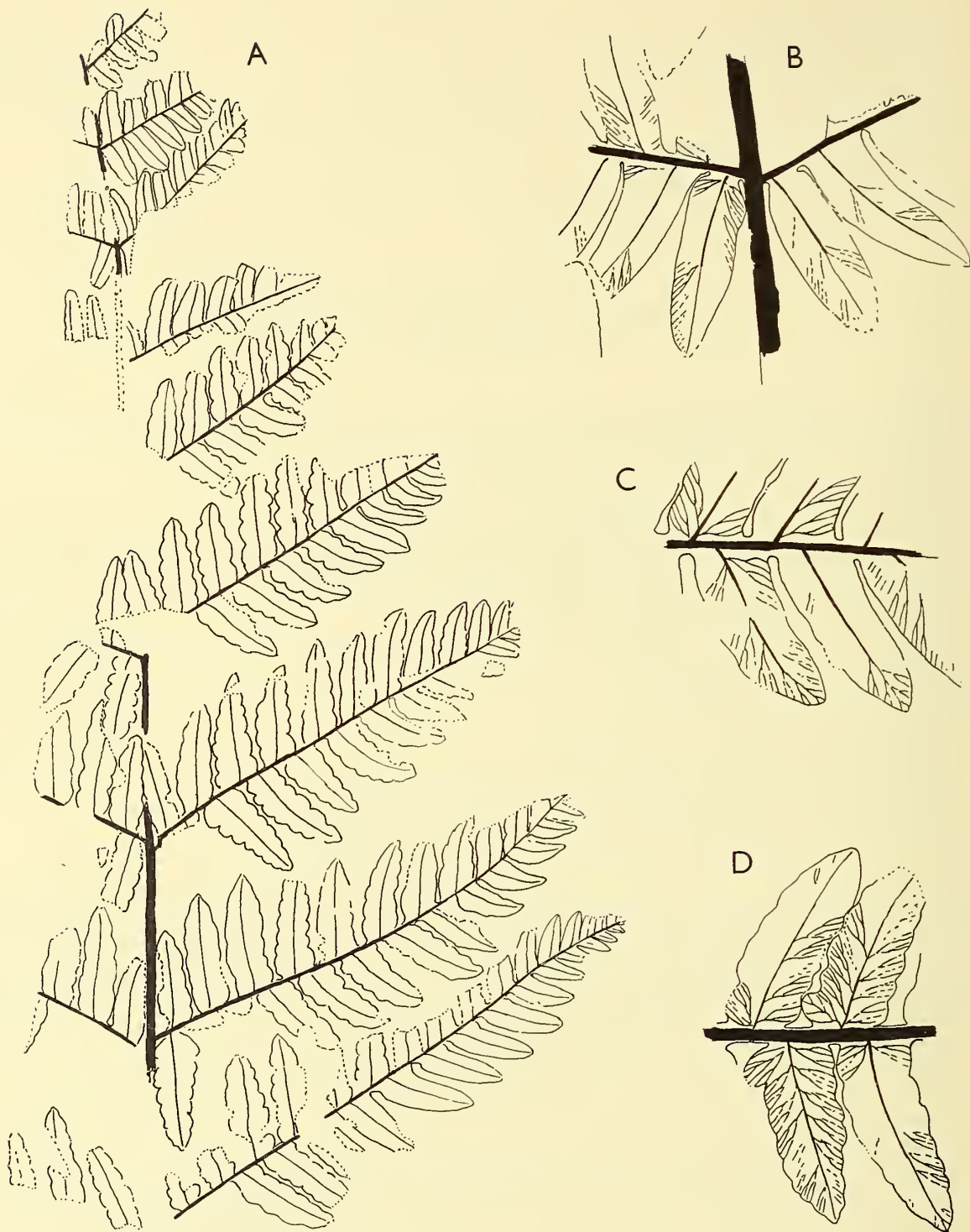


Fig. 69. *Cladophlebis haiburnensis* (L. & H.)

A, largest specimen, V.32511, $\times 1$. Fragments of two other pinnae occur at about 3 cm. and about 6 cm. below the lowest shown. B, part of the rachis and pinnules of V.32512, $\times 2$. C, upper pinnules from A, $\times 2$. D, lower pinnules from A, $\times 2$.

The specimens are from Beast Cliff *Otozamites* Bed.

- 1929 *Cladophlebis haiburnensis* (L. & H.): Yabe & Oishi, p. 5, pl. 1, fig. 2; pl. 3, fig. 1. (Indeterminable fragments. Shantung.)
- 1930 *Cladophlebis haiburnensis* (L. & H.): Turutanova-Ketova, p. 321, pl. 1, fig. 1; text-fig. 2. (Distinct, more like *C. aktashensis*. Jurassic; Kirghiz.)
- 1931 *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 237, pl. 17, fig. 2. (? *C. aktashensis*. Kita Otari, Japan.)
- 1931 *Cladophlebis haiburnensis* (L. & H.): Prinada, p. 13, pl. 1, figs. 10, 11; pl. 2, fig. 26. (Indeterminable small fragments. Central Asia.)
- 1932 *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 281, pl. 24, figs. 1-3; pl. 26, figs. 1, 2. (= *C. aktashensis*. Nariwa, Japan.)
- 1932b *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 56. (Record from Nagati, Japan. No figure.)
- 1932a *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 6, pl. 1, fig. 6, pl. 2, fig. 2. (= *C. aktashensis*. Shitaka, Japan.)
- 1933 *Cladophlebis haiburnensis* (L. & H.): Kryshstofovich & Prinada, p. 15, text-fig. 1. (? Distinct, pinnae large and crowded. Urals.)
- 1933 *Cladophlebis haiburnensis* (L. & H.): Yabe & Oishi, p. 208, pl. 30, fig. 12; pl. 31, figs. 4, 4a, 5; pl. 32, figs. 1, 2. (? = *C. aktashensis*. Manchuria.)
- 1935 *Cladophlebis haiburnensis* (L. & H.): Brick, p. 21, pl. 3, fig. 1; text-figs. 8, 9. (Distinct, rachis punctate; pinnae alternate, crowded. Ferghana, Central Asia. List of references.)
- 1941 *Cladophlebis* cf. *haiburnensis* (L. & H.): Brick, p. 20, pl. 6, fig. 1; text-fig. 3. (Indeterminable fragments. Uzbekistan.)
- 1956 *Cladophlebis haiburnensis* (L. & H.): Semaka, p. 112, text-figs. 5, 20-23. (? Distinct, pinnule base contracted. Lias; Roumania.)
- 1876 *Asplenium (Diplazium) spectabilis* Heer, p. 96, pl. 21, figs. 1, 2a, 2c, 2d. (Indeterminable. Siberia. Has sometimes been referred to *C. haiburnensis*; also *C. spectabilis* (Heer) Fontaine, 1889, p. 345, pl. 49, figs. 4, 5. (Distinct. pinnae at smaller angle.)

Brick (1935: 21) cites several other Russian references not available to me.

EMENDED DIAGNOSIS. Lamina as a whole lanceolate; width typically about 16 cm., length unknown (exceeding 30 cm.), apex acute. Petiole unknown; rachis slender, not channelled, not punctate, without hairs, marked with very close longitudinal cell-striae, 10 μ apart. Pinnae arising laterally and usually opposite, at intervals of up to 3 cm. and at an angle of about 80° in the middle region of the leaf. Pinna rachis very slender, smooth, not channelled. First pinnule arising on the basiscopic side close to the main rachis, later ones alternating katepistomically. Typical pinnules arising at 80°-90° (rather less distally), but basal ones tending to be parallel with main rachis. Basal pinnules often rather small but otherwise unspecialised. Pinnules on the two sides of the pinna equal, only overlapping pinnules of adjacent pinnae to a slight extent. Pinnules usually in contact with their neighbours but sometimes 1 mm. apart. Pinnule lanceolate, nearly straight or only slightly curved forwards; apex obtusely pointed, base typically slightly contracted, especially in larger pinnules. Margins entire in smaller pinnules, sometimes more or less divided into rounded lobes in larger ones. Midrib nearly straight and median; lateral veins for the most part forked twice. Lowest lobe on basiscopic side of large pinnules occasionally forming a spur with a midrib of its own. Texture of lamina moderately dense, lamina otherwise flat.

DISTRIBUTION. The Yorkshire localities (Haiburn Wyke, Beast Cliff and Whitby) are Lower Deltaic. The similar-looking leaves from Greenland and Sweden are Lower Liassic, those from Korea are of an undetermined stage of the Lower Jurassic.

DISCUSSION. *C. haiburnensis* is rare in Yorkshire. Only two old specimens are known, the holotype in the Hancock Museum at Newcastle, and a very similar specimen (no. K80) in the Sedgwick Museum, Cambridge. Both are preserved in a hard brown ironstone and localised as from Haiburn Wyke. I have not found it at Haiburn, but it occurs some distance north in the Beast Cliff *Otozamites* Bed where I collected six leaves showing the rachis. There are also four

fragments from Whitby. The twelve best agree in their slender rachises and spreading pinnae, but in one apex from Whitby the pinnae alternate. The venation is uniform, except in the largest pinnules which have a slightly lobed margin. The most strongly lobed of all are figured, but these pinnules seem exceptional.

The rachis is very finely striated in all specimens and in none is it at all punctate. As these features are constant in the known Yorkshire specimens I regard them as diagnostic, and this results in a different conception of the species from that hitherto held. This concept is based on the work of Seward & Thomas (1911) which is a synthesis of true *C. haiburnensis* with an Asiatic species which *might* have fallen in the range of the Yorkshire material, but now that enough specimens are available to show this range, fairly certainly does not. Accordingly, many records have been rejected and *C. haiburnensis* thus restricted becomes a rare species. The only identifications accepted are those specimens which agree in their slender, non-punctate rachis and opposite, rather remote pinnae arising at a large angle. Specimens which do not show their rachis are regarded as indeterminable. It may be recalled that Oishi (1940: 267) already recognised that more than one species was included in *C. haiburnensis*.

The Korean specimens described by Kawasaki (1926, 1939) agree in the character of the rachis and branching, but have slightly smaller pinnules (within the range of the Yorkshire material). None shows the large lobed form. The Greenland specimens described as *C. ingens* (Harris 1931, 1937) agree well but are rather fragmentary.

It may be pointed out that some of the magnificent specimens of *Cladophlebis nebbensis* described by Johanssen (1922) are far more like the Yorkshire holotype of *C. haiburnensis* than are most of the specimens identified with this species. None, however, has lobed pinnules, associated specimens with lobed pinnules being described under other names. *C. nebbensis* of Brick (1935: 16, pl. 1, fig. 7) is also similar. As a rule the name *C. nebbensis* has been restricted to specimens with rather smaller pinnules than *C. haiburnensis*.

Some of the South American specimens of *Cladophlebis mesozoica* Kurtz figured by Frenguelli (1947, pl. 7, figs. 3, 6) also look similar. In the diagnosis, however, the pinnae are stated to be alternate. Another similar form is *Asplenium whitbiense* Heer (1876a: 94, pl. 20, fig. 1) from Amurland.

It is to be regretted that this long-established Yorkshire species is still unknown fertile and therefore unclassifiable botanically.

Cladophlebis aktashensis Turutanova-Ketova

Text-fig. 70

None of the following is from Yorkshire.

- ?1906 *Todites williamsoni* Brongn.: Yokoyama, p. 28, pl. 8, fig. 1. (Similar leaf. China.)
- ?1922 *Cladophlebis haiburnensis* (L. & H.): Yabe, p. 16, pl. 2, figs. 9-11; text-figs. 12-16. (Similar leaves. China and Korea.)
- 1930 *Cladophlebis aktashensis* Turutanova-Ketova, p. 322, pl. 3, fig. 7; pl. 4, fig. 7; pl. 5, fig. 8; text-fig. 1. (Middle Jurassic; Kirghiz.)
- ?1930 *Cladophlebis haiburnensis* (L. & H.): Turutanova-Ketova, p. 321, pl. 1; text-fig. 2. (As above.)
- 1932 *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 281, pl. 24, figs. 1-3; pl. 26, figs. 1, 2. (Fine leaves. Jurassic; Nariwa, Japan.)
- 1932a *Cladophlebis haiburnensis* (L. & H.): Oishi, p. 6, pl. 1, fig. 6; pl. 2, fig. 2. (Middle Jurassic; Shitaka, Japan.)
- 1935 *Cladophlebis aktashensis* Turutanova-Ketova: Brick, p. 19, pl. 1, fig. 3; text-fig. 6. (Ferghana, Central Asia.)

EMENDED DIAGNOSIS. (Based partly on Japanese specimens). Leaf large, length of lamina estimated at 1 m. or more (Oishi, 1932), width probably 50 cm. Rachis stout, up to 10 mm. thick, smooth, not channelled but showing obscure longitudinal ridges and cellular striae 20μ apart. Pinnae arising laterally; lower ones almost at right angles, but angle of origin about 70° in middle of leaf and about 45° in the upper part. Pinnae sometimes sub-opposite, but usually

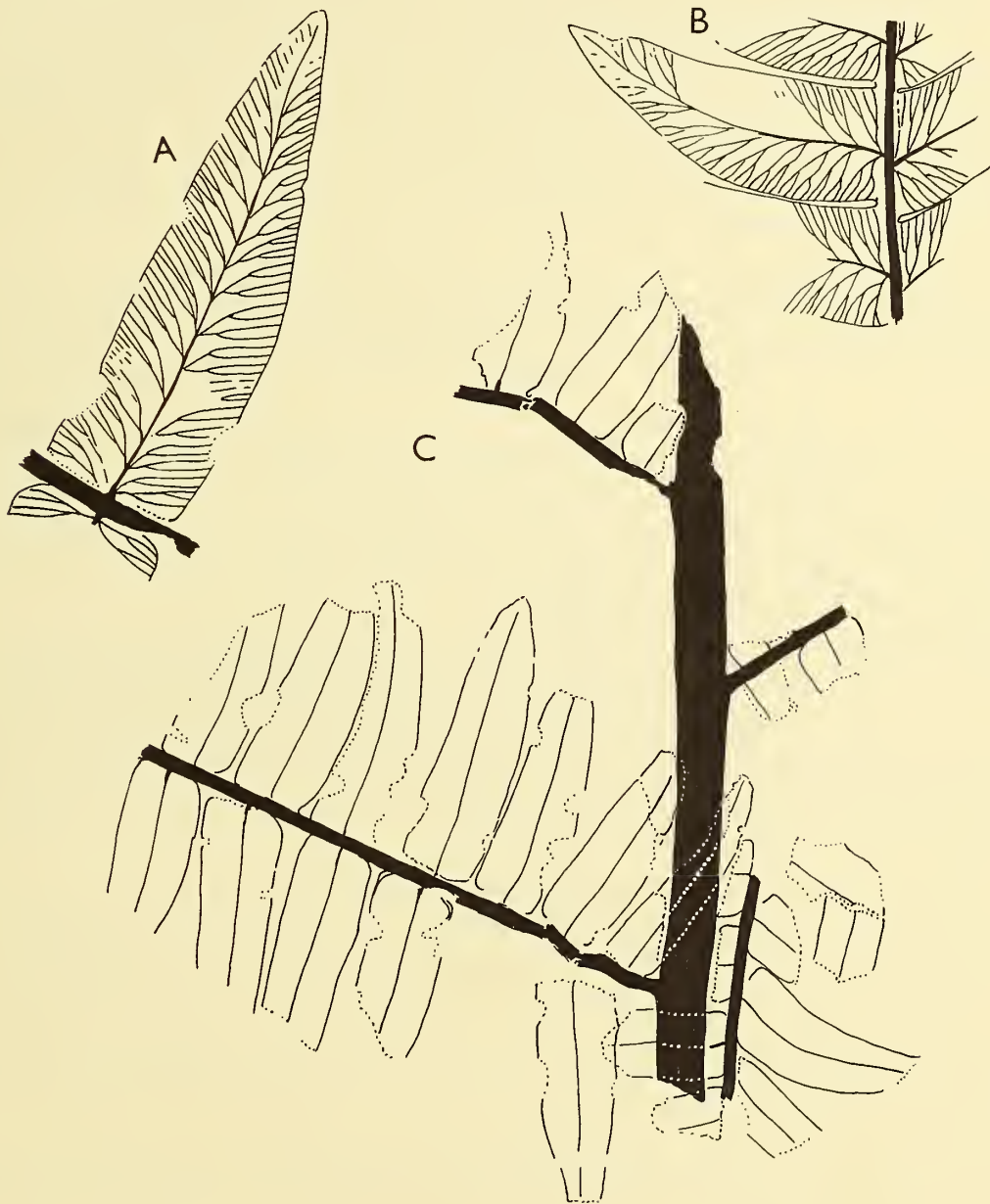


Fig. 70. *Cladophlebis aktashensis* Turutanova-Ketova

A, pinnule from C, $\times 2$. B, pinnules from distal part of an isolated pinna, V.32509. $\times 2$.
C, largest fragment (drawn from part and counterpart), V.32510, $\times 1$.

The specimens are from Roseberry Topping (Lower Deltaic.)

alternate, pinna rachis stout, typically 2 mm. wide, not channelled, without hairs. Lamina of one pinna overlapping adjacent pinnae. Pinnules on the two sides of a pinna equal, first pinnule arising on basiscopic side; basal pinnules unspecialised but tending to lie along the rachis. Pinnules remaining equal in size for a considerable distance from the rachis, but gradually becoming more acute and forward-pointing. Largest pinnules about 34 mm. \times 10 mm., typical size about 25 mm. \times 7 mm. In the largest pinnules base slightly contracted, margins entire, apex obtusely angular or rounded; in smaller distal pinnules base not contracted, margins entire, apex acute; margins of adjacent pinnules of a pinna often close but seldom overlapping. Midrib nearly straight, lateral veins almost all forked twice, vein branches ending in the margin at a concentration of 18–24 per cm., and an angle of about 70°. Substance of lamina moderately dense, veins not very conspicuous; margins flat.

DISTRIBUTION. The Yorkshire specimens are Lower Deltaic. The Russian and Asiatic specimens all appear to be from the Middle or Lower Jurassic.

DISCUSSION. This species is represented by two fairly good fragments, both figured, and a number of smaller ones all from Roseberry Topping (Hamshaw Thomas Colln.). It appears to be frequent in certain bedding planes. The species has not been previously recognised outside Russia and Northern Asia having been confused with *C. haiburnensis*. It may be widespread.

The Yorkshire specimens agree well with Turutanova-Ketova's type material, though none of her leaves has quite such large pinnules, nor such distant pinnae as the largest Yorkshire specimen. Her drawing shows the apex of the pinnule as rounded but several in her photographs have obtusely angular apices similar to that shown in Text-fig. 70. Only one of the larger Yorkshire pinnules shows its apex well; certain others appear to show a rounded apex but this is due to imperfect preservation.

Oishi's fine series of specimens are also very similar, though again none has pinnules as large as the largest Yorkshire specimen. Oishi (1932a: 281) describes the pinnae as sub-opposite, arising at almost a right angle and the pinnules as obtusely rounded, but his figures show that these features are not constant and do not constitute a difference from the present specimens.

COMPARISON. *C. aktashensis* has been confused with *C. haiburnensis* and agrees with it (particularly its forked veins) in several respects.

Differences are: *C. aktashensis*: rachis stout, 6 mm. thick (Yorkshire) or up to 10 mm. (Japan), with striae surface cells 20 μ wide; in *C. haiburnensis*: rachis slender, up to 2 mm. thick, surface cells 10 μ wide. Pinnae in *C. aktashensis* variable, most often alternate and arising at an angle of about 70° or less, and sufficiently crowded for the pinnules to overlap the adjacent pinnae considerably. In *C. haiburnensis* pinnae arising opposite and at an angle of 80° or more and only slightly overlapping the next pinnae. The pinna rachis is nearly 2 mm. wide in *C. aktashensis* and less than 1 mm. in *C. haiburnensis*.

In *C. aktashensis* the pinnules may reach a large size (35 mm. \times 11 mm.), but even large ones have an entire margin. In *C. haiburnensis* they reach 17 mm. \times 7 mm., and the larger ones have a distinctly lobed margin.

The veins are very similar and end in the margin at 18–25 per cm., except in specimens of *C. haiburnensis* where the margin is strongly lobed. (Turutanova-Ketova figures the veins of *C. haiburnensis* as rather less crowded but I think her specimen is merely a form of *C. aktashensis* with expanded pinnules.

Form-Genus SPHENOPTERIS Sternberg, 1825:15

Sphenopteris metzgerioides Harris

Text-fig. 71

- 1864 *Sphenopteris Jugleri* Ett.: Leckenby, p. 79. (Brief reference to present specimen.)
 1875 *Sphenopteris Jugleri* Ett.: Phillips, p. 218, lign. 40. (Rough figure of present specimen.)
 1894 *Ruffordia Goepperti* (Dunker): Seward, pp. 77, 78, in part. (Reference to present specimen only.)
 1900 *Ruffordia Goepperti* (Dunker): Seward, p. 133, in part. (Reference to present specimen only.)
 1946a *Sphenopteris metzgerioides* Harris, p. 825, text-fig. 3. (Figures repeated here.)

EMENDED DIAGNOSIS. (Based on the holotype). Leaf (in part known) triangular and about 7 cm. long, 7 cm. broad, tripinnate. Rachis slender, not channelled. Primary branches nearly opposite, arising at an angle of about 45° , secondary branches becoming alternate rather irregularly, ultimate branching by nearly equal dichotomy. Branches crowded and overlapping. Secondary and tertiary rachises flanked by a continuous lamina, lamina widest (about 0.5 mm.) on primary rachis, gradually narrowing to 0.15 mm. wide on terminal branches. Margins entire, apices rounded; segments with a single vein, vein ending just below the apex. Lamina delicate, everywhere composed of a single layer of cells about 50μ long, 40μ broad, but midrib containing a number of narrow cells in addition to an epidermis of cells like the lamina. No cuticle present, no hairs seen.

HOLOTYPE. K.158, Leckenby Coll., Sedgwick Museum, Cambridge.

OCCURRENCE. *S. metzgerioides* is imperfectly localised. The locality label 'Lower Shale, Scarboro' has no precise meaning. Phillips records it as 'lower shale, Stainton dale'. It cannot be from the Dale at Stainton because there is no Lower Deltaic exposed, but it could be from the neighbouring valley at Haiburn, or from Beast Cliff, east of Stainton Dale. I have not, however, seen a matrix particularly like it in that district, though it does look much like that of the Gristhorpe Bed, and it is associated with *Nilssoniopteris vittata*, one of the commonest Gristhorpe Bed leaves. Its exact origin must be considered unknown.

DISCUSSION. The species is represented by the holotype only. Leckenby Coll. No. 144 mentioned by Seward (1900: 133) is *Coniopteris murrayana*. A re-examination of the holotype confirms the previous interpretation of the lamina (Harris, 1946a: 827) as being composed of a single layer of cells. It has been compared with the lamina of species of *Coniopteris* which in some states of preservation look equally delicate, but in them it is always clear that more than one set of cells exist. The cells are only visible when the specimen is immersed in oil. In most parts the contents of the cells form dark masses separated by paler walls, but in places the walls are darker than the contents. There is nowhere any suggestion of other cell layers in the lamina. Similar preservation was noticed in the indusium of *Coniopteris bella*, also composed of a single cell layer. The crowded branches overlap and many of them are broken off or hidden. Several secondary branches thus appear one sided but probably the branching was originally symmetrical. The order of branching is notably irregular, here anadromic, there katadromic.

This fern agrees with many species of *Hymenophyllum* in form and in the structure of the lamina, and, as far as known, it is the only fossil fern with a one-layered lamina. A few small sterile or fertile fern fragments have been referred to *Hymenophyllites* of the Hymenophyllaceae, mostly from the Carboniferous, and two from the Upper Lias by Raciborski (1894). These Liassic species, though perhaps correctly placed, show no characters which exclude the possibility that they might be *Coniopteris* fragments (for example *Coniopteris bella* with a sorus

rather like *Hymenophyllum*). *S. metzgerioides* is not classified in the Hymenophyllaceae, because although the lamina is like *Hymenophyllum* there is no supporting evidence.

SPECIFIC COMPARISON. The only Yorkshire species which could be confused with *S. metzgerioides* are *Stenopteris williamsoni*, *S. nitida* (both of which have a cutinised lamina several cells thick), *Coniopteris bella* and perhaps other species of *Coniopteris* (in fragments)

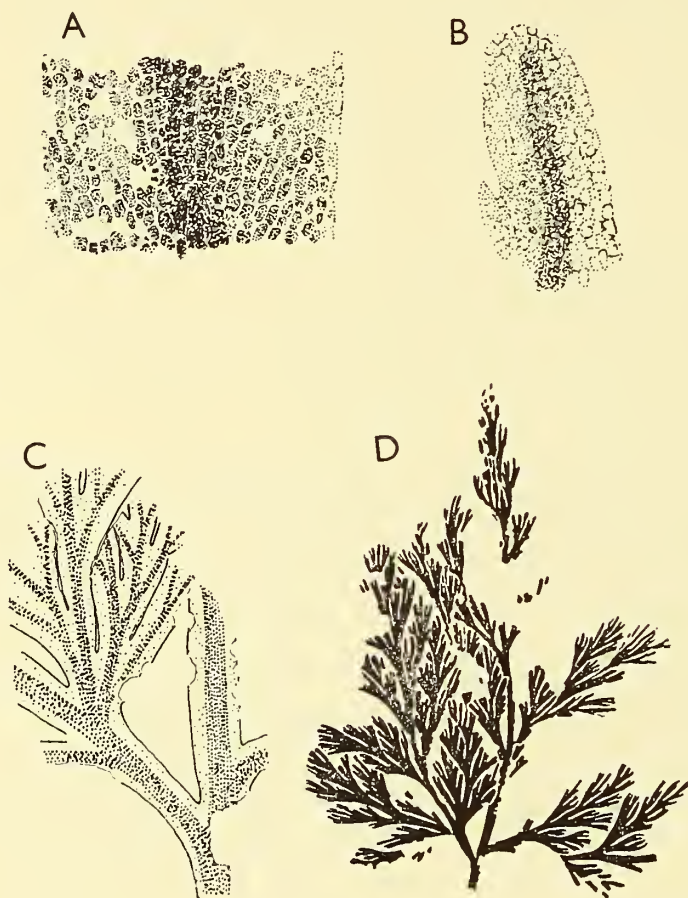


Fig. 71. *Sphenopteris metzgerioides* Harris

A, part of a leaf segment in which the cells are represented by their dark contents, $\times 60$. B, apex of leaf segment, cell walls preserved, $\times 40$. C, part of main rachis and base of a pinna, showing the veins, $\times 4$. D, whole specimen, $\times 1$. All figures are from the holotype, K.158, Leckenby Coll., Sedgwick Museum, Cambridge, and are reproduced from Harris (1945, text-fig. 3).

where the pinna is narrower, and again the lamina more than one cell thick. Comparison with various incompletely known species of other regions is possible but unfruitful; mention must, however, be made of *Ruffordia goepperti* (Lower Cretaceous) with which this specimen had been identified. Certain leaves of *Ruffordia* look just like *S. metzgerioides* but they differ greatly in structure, the lamina is usually dense, and even when reduced to a pale colour is seen to be several cells thick. Another difference is that the lobe apices are acute or mucronate.

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